FACTORS AFFECTING BODY MASS OF PREFLEDGING EMPEROR GEESE

By

Bryce Cameron Lake

RECOMMENDED:

Joel A. Schmutz

Christa P.H. Mulder

Mark S. Lindberg, Advisory Committee Chair

Chair, Department of Biology and Wildlife

APPROVED:

Dean, College of Natural Science and Mathematics

Dean of the Graduate School

May 17, 2005

Date

FACTORS AFFECTING BODY MASS OF PREFLEDGING EMPEROR GEESE

A

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Bryce Cameron Lake, B.S.

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Abstract: Body mass of prefledging geese has important implications for fitness and population dynamics. To address whether interspecific competition for forage was broadly relevant to prefledging emperor geese, I investigated the factors affecting body mass at three locations across the Yukon-Kuskokwim Delta, Alaska. From 1990 – 2004, densities of cackling geese more than doubled and were ~2 – 5x higher than densities of emperor geese, which were relatively constant over time. During 2003 – 2004, body mass of emperor geese increased with net above-ground primary productivity (NAPP) and grazing lawn extent and declined with interspecific densities of geese (combined density of emperor and cackling geese). Grazing by geese resulted in consumption of ≥ 90% of the NAPP that occurred during the brood rearing period, suggesting that interspecific competition was due to exploitation of common food resources. At six sampled locations, grazing lawn extent varied among- and within-locations, and was stable or declined slightly during 1999 – 2004, indicating reduced per capita availability. I conclude that negative effects of interspecific goose densities on body mass of prefledging geese are partially responsible for recent declines in the fall age ratio of emperor geese because of a positive correlation between body mass and survival to fall staging areas. Management to increase the population size of emperor geese should consider interspecific densities of geese and interactions between interspecific densities and forage.

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PREFACE

Dear Reader,

The body of this thesis comprises two manuscripts, each prepared for submission to different journals. Chapter 1 was prepared for publication in *Arctic*, and chapter 2 was prepared for publication in *Auk*. Although each manuscript has coauthors listed, I was responsible for the analysis, interpretation, and reporting of these data. Thus, I take full responsibility for any errors in this work. The "we" contained in these manuscripts refers only to me and my coauthors.

The collection, analysis, and interpretation of these data, however, would not have been possible without the tremendous support of my committee members, Mark Lindberg, Joel Schmutz, and Christa Mulder. Mark has been supportive of my research endeavors since I was an undergraduate, and it was fortunate that I was able to work with him on a graduate project. In addition to his role as an advisor and mentor, he exposed me to the process of science and the level of rigor at which science needs to be conducted. I initially met Joel at the 2000 Alaska Bird Conference where he watched me give my first presentation and later hired me as a summer technician. He encouraged me to pursue graduate school, and when I proposed working on a graduate project with him, he never wavered. While training students is not an official part of Joel's job, he routinely does so, and I am thankful for this. Aside from his guidance on research design and data analysis, Joel taught me, perhaps most importantly, how to think more broadly about ecological issues. I look forward to future collaborations with Mark and Joel.

Christa provided valuable insight, editing, and brought a needed, broader perspective to this project.

This project would not have been possible without the financial, logistical, and technical support of several organizations and many individuals. Mike Rearden and Fred Broerman from the Yukon Delta National Wildlife Refuge sponsored this research and are thanked for sticking with me after an initial failed field season. Their loyalty contributed to the success of this project and should be used as a benchmark for collaborations between universities and agencies. Fred deserves special recognition because, in addition to logistical coordination and field assistance, he was able to obtain permission to conduct research at Kokechik Bay. Other financial and logistical support was provided by the Alaska Science Center (ASC), and Mike Anthony and Craig Ely from the ASC deserve additional recognition. Mike conducted the videography each year, and Craig led the collection of data at Old Chevak. Direct financial support was provided by the Yukon Delta National Wildlife Refuge, the Department of Biology and Wildlife, Institute of Arctic Biology, and Graduate School, University of Alaska Fairbanks, and the California Waterfowl Association – Dennis Raveling Scholarship.

Because of its remote nature, working on the Yukon-Kuskokwim Delta necessitates the use of aircraft, and I thank Paul Liedberg, Mike Rearden, George Walters, Gene Peltola, and Paul Anderson for many safe hours of flying. I incorporated data collected annually by United States Fish and Wildlife Service – Migratory Bird Management, and Bill Eldridge, Julian Fischer, and Bob Platte are thanked for providing these data. Karen Enochs, Michelle Das, and Kathy Pearse from the Alaska Cooperative

Fish and Wildlife Research Unit, Marta Conner from the Institute of Arctic Biology, and Carol Piser from the Department of Biology and Wildlife are thanked for, among other things, making sure that I got paid and was able to travel to conduct field work and attend meetings. I thank Myron Naneng and the Sea Lion Corporation for access to private lands.

My time as a graduate student was enhanced considerably by interactions with fellow students. I benefited from discussions and hours of problem solving with John Citta, Steve Hoekman, Kate Martin, Brandt Meixell, Dave Safine, Josh Schmidt, and Johann Walker. In particular, I would like to acknowledge Steve and Johann. For two years, I had the opportunity to sit between, and learn directly from these two incredibly intelligent individuals. Former UAF graduate students Brian Person, Mark Herzog, and Chris Nicolai are thanked for assistance with data analysis and interpretation.

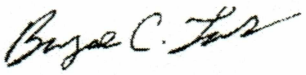
During the summer, I was fortunate to work with many competent, hard-working field technicians. These individuals are thanked for their tireless data collection and ability to maintain a positive attitude in spite of rain, mud, wind, and whatever else we were faced with (e.g., broken boat engines). Persons who contributed $\geq$ 2 years of work included Jeff Ball, Erin Bohman, Charles Eldermire, Trish Fontaine, and Marnie Shepherd.

I never would have gotten a start down this career path without the help of a few folks. Mike Woods taught me early on the value of hard work and how to market myself. Eric Taylor and Eric Rexstad took a chance on a naive undergraduate and gave me my

first paid field job. My experience leading to graduate school benefited from nights of studying with David Bump, Jason Caikoski, and Nate Pamperin.

My parents, Liz and Chris Lake, deserve the most recognition. In addition to providing me with a staging area every spring on my way to the field, their support and love during my academic career provided the stimulus I needed to succeed.

Sincerely,



Bryce C. Lake

INTRODUCTION

The Yukon-Kuskokwim Delta, Alaska is the breeding ground for nearly all of the world's emperor geese (*Chen canagica*), cackling geese (*Branta hutchinsii*), and Pacific black brant (*B. bernicla nigricans*) as well as an important breeding area for greater white-fronted geese (*Anser albifrons*) (King and Derksen 1986). Populations of all four species declined precipitously from the 1960's to the mid 1980's, prompting the United States Fish and Wildlife Service to implement harvest restrictions on both breeding and wintering areas (Raveling 1984, Sedinger 1996). Since 1985, populations of cackling and greater white-fronted geese increased at ~ 8% per year, although the increase in cackling geese has slowed since about 1996, and some local populations of black brant have increased, while numbers of emperor geese have remained at a constant, depressed level, well below management goals (Eldridge 2003).

Population size is a function of four processes: immigration, emigration, survival, and productivity (Gotelli 1998). Overall, at a regional scale, immigration and emigration likely make little contribution to the population dynamics of emperor geese because ≥90% of the world's population breeds on the Yukon-Kuskokwim Delta (King and Derksen 1986). Apparent survival of adult female emperor geese is high (~ 81% annually; Schmutz and Morse 2000) and has exhibited little to no variation during the period 1985 – 2003 (Schmutz et al. 1994, Schmutz and Morse 2000, J. Schmutz unpubl. data). In contrast, the number of juvenile emperor geese in the fall population is low relative to other goose species (Timm and Dau 1979, Ely et al. 1993), implying low productivity. A notable concern is that the fall age ratio, an index of productivity and

juvenile survival, has been particularly low during 1996 – 2003, as compared to 1985 – 1995 (Figure 1; Anderson et al. 2003). Virtually every study that has investigated survival of juvenile geese (Sedinger et al. 1995, Van Der Jeugd and Larsson 1998, Cooch 2002, Reed et al. 2003), including emperor geese (Schmutz 1993), has detected a strong positive correlation with body mass just prior to fledging. As such, it is reasonable to expect that variation in body mass has large influence on the number of juveniles surviving to fall.

Some evidence suggests that body mass of prefledging emperor geese has declined from previous levels, and that this decline may be from interspecific competition for forage (Schmutz and Laing 2002). Broods of emperor geese, black brant, and cackling geese all forage in *Carex subspathacea* grazing lawns (Schmutz and Laing 2002). A recent study (Schmutz and Laing 2002) documented that time spent foraging and body mass of prefledging emperor geese increased over time, and that these increases were most strongly related to the collective density of all goose species (not just emperor geese), which included cackling geese and black brant. Nonetheless, the limited spatial scope of this research questions its applicability across broader geographic scales, such as the Yukon-Kuskokwim Delta.

The overall objective of my research was to investigate large-scale variation in the factors affecting body mass of prefledging emperor geese on the Yukon-Kuskokwim Delta. In this thesis, I present these results in two parts.

In the first part (Chapter 1), I investigated the utility of aerial videography (Anthony et al. 1995, Person et al. 2003) for assessing large-scale spatial and temporal

variation in the percent aerial coverage or extent of *C. subspathacea* grazing lawns, the primary food of prefledging emperor geese (Laing and Raveling 1993, Schmutz 2001). The extent of this food resource is dynamic (Person et al. 2003), in part due to interactions with consumers (Ruess et al. 1997, Person et al. 2003). Videography surveys were conducted in 1999, 2003, and 2004 at six locations, encompassing ~ 40% of the North American population of breeding emperor geese (B. Lake unpubl. data). I hypothesized that the extent of grazing lawns was stable or may have declined from 1999 – 2004, among- and within-locations.

In the second part (Chapter 2), I investigated spatial and temporal variation in body mass of prefledging emperor geese. Sampling was conducted at three locations during 1990 – 2004. At each location and in each year, I estimated species-specific goose densities (emperor and cackling Geese), and during 2003 – 2004, I also estimated food availability, as represented by net above-ground primary productivity (NAPP) and spatial extent of *C. subspathacea* grazing lawns. I hypothesized that body mass of prefledging emperor geese was related to interspecific densities of geese (emperor and cackling geese) and availability of food.

Collectively, these two chapters were intended to increase our understanding of the degree to which body mass of prefledging emperor geese may be affected by interspecific competition for forage. Because these geese species are managed differentially when not sympatric on breeding grounds, detection of such variation across larger spatial and temporal scales has implications for management at a continental scale.

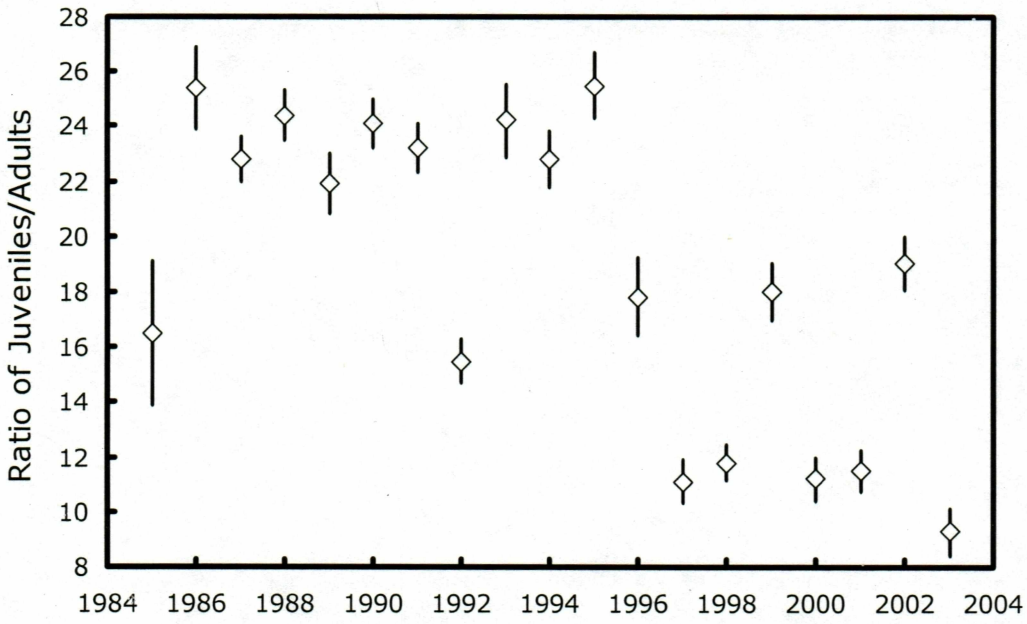


Figure 1. The ratio ($\overline{X} \pm SE$) of juvenile to adult emperor geese observed during fall on the Alaska Peninsula from 1985 – 2003, estimated with aerial photographic counts (adapted from Anderson et al. 2003).

Large-scale variation in extent of grazing lawns used by Emperor Geese, estimated with videography[1]

ABSTRACT. The ability to detect fine-scale habitats across a broad spatial scale provides the opportunity to examine interactions between consumers and resources at a population level. We assessed the utility of aerial videography for examining large-scale variation in an important food resource used by broods of emperor geese (*Chen canagica*). Sampling was conducted in 1999, 2003, and 2004 at six locations, encompassing ~ 40% of the North American population of breeding emperor geese. We investigated the hypothesis that the percent aerial coverage or extent of grazing lawns was stable or declined during 1999 – 2004, among- and within-locations. Classification accuracy for grazing lawn habitats was >91%. We detected stability or a slight decline in grazing lawn extent from 1999 – 2004, among- and within-locations. Grazing lawn extent varied among locations; mean estimates (± SE) ranged from 1.8% (0.7) to 7% (0.7). Within locations, grazing lawn extent was 4% (SE = 0.8) higher adjacent to ponds than rivers. Overall, videography is a useful method to quickly sample across a large region quickly and accurately identify fine-scale habitats. Large-scale variation in grazing lawn extent likely contributes to patterns of variation in body mass of prefledging emperor geese, which has a demonstrated demographic effect. Management plans for

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[1]Prepared for *Arctic* as Lake, B. C., M. S. Lindberg, J. A. Schmutz, R. M. Anthony, and F. J. Broerman. Large-scale variation in extent of grazing lawns used by Emperor Geese, estimated with videography.

emperor geese should consider consumer-resource interactions on the Yukon-Kuskokwim Delta, Alaska.

INTRODUCTION

Recruitment and reproductive performance in birds are strongly linked to foraging opportunities and the availability of food resources (Lack, 1947, 1948; Williams et al., 1966; Rohwer, 1992), and spatial and temporal variation in these metrics can strongly affect fitness. Assessment of the degree to which populations are limited by food resources, however, requires knowledge of variation in availability across a broad spatial scale.

Satellite-based remote sensing is commonly used for assessing variation in land cover (Foody, 2002; Stow et al., 2004) and presents a suite of methods for quantifying food availability across a large scale. In situations where higher resolution is needed, videography is an attractive alternative to remote sensing because it can detect finer-scale, patchily distributed features (Markus et al., 2003) and also can be applied across a large spatial scale. Further, these capabilities provide the opportunity to examine interactions between fine-scale food resources and consumers at a population level. Such interactions have relevance for life-history of birds (Martin, 2004), especially herbivorous species like geese (Sedinger, 1997), for which growth and survival of young is strongly tied to availability of food resources (Owen and Black, 1989; Sedinger et al., 1995; Reed et al., 2003).

In Arctic and sub-Arctic ecosystems, geese are primary consumers during the summer months (Kerbes et al. 1990; Gauthier et al., 2004) when they heavily graze

vegetation high in nitrogen (Cargill and Jefferies, 1984; Person et al., 1998). For instance, in *Carex subspathacea* grazing lawns, geese remove over 95% of the net above-ground primary productivity each summer (Person et al., 1998; Person and Ruess, 2003). This plant is found throughout Arctic salt-marsh ecosystems (Hultén, 1990), yet a means to quantify its availability across a large-scale has remained elusive, likely owning to its patchy distribution. For example, the size of these grazing lawns is variable and ranges from 10cm wide, linear strips to 0.25km^2 patches (Person et al., 1998).

At a single colony location for black brant (*Branta bernicla nigricans*), it was noted that videography used for estimating the abundance of nests (Anthony et al., 1995) could be used to identify fine-scale plant communities, such as grazing lawns, although the accuracy at which they were identified was not investigated (Person et al., 2003). The motivation for our study was to employ these videography techniques across a large landscape to assess large-scale spatial and temporal variation in grazing lawns, and to evaluate the utility of videography with ground-truthing data.

On the Yukon-Kuskokwim Delta, Alaska broods of black brant, emperor geese (*Chen canagica*), and cackling geese (*B. hutchinsii*) all forage in grazing lawns (Schmutz and Laing, 2002). The percent aerial coverage or extent of grazing lawns is dynamic, in part due to interactions with consumers, and Person et al. (2003) documented an increase in the extent of grazing lawns during 1991 – 1999, to which they attributed an increase in growth of black brant goslings. However, the area sampled by Person et al. (2003) was relatively small, and may not be reliable for inferring interactions between resources and consumers at a larger spatial scale. Because $\geq$ 90% of the world's population of emperor

geese breeds on the Yukon-Kuskokwim Delta (King and Derksen, 1986; Petersen et al., 1994), variation in grazing lawn extent across this landscape has relevance at a population level. Furthermore, the population size of emperor geese is well below goals set by managers, and recent declines in productivity (Anderson et al., 2003) are suggestive of reduced per capita availability of grazing lawns and growth of goslings (Schmutz and Laing, 2002).

We used aerial videography to examine large-scale spatial and temporal variation in the extent of grazing lawns. We conducted sampling at six locations, which encompassed approximately 40% of the North American breeding population of emperor geese (B. Lake unpubl. data). The extent of grazing lawns has been positively associated with grazing pressures (Ruess et al., 1997) and a positive feedback with densities of the herbivore population, with a four-year time lag (Person et al., 2003). We investigated the hypothesis that grazing lawn extent was stable or may have declined during 1999 – 2004 because of relative stability in the population size of the composite goose community (Anthony, 2004; Eldridge, 2003) coupled with recent years of low nest success (Fischer et al., 2004), which substantially reduced brood numbers needed for maintaining grazing lawns. Previous researchers have documented spatial variation in forage availability and its importance to growth of prefledging geese (Cooch et al., 1993; Sedinger et al., 2001; Herzog, 2002), and we also examined whether grazing lawn extent varied among- and within- locations.

STUDY AREA

We conducted videography sampling across the outer fringe of the Yukon-Kuskokwim Delta, Alaska. This region is a coastal saltmarsh maintained by large-scale flooding events and daily influxes of brackish water from the numerous rivers and sloughs permeating the landscape (Kincheloe and Stehn, 1991). Species diversity of vegetation is low, and continuous meadows of *C. ramenskii* and *C. rariflora* dominate the landscape (Babcock and Ely, 1994; Jorgenson, 2000). Along the interface of *C. ramenskii* meadows and also along coastal margins, riparian mudflats, and pond margins are patchily distributed swards of *C. subspathacea* (Kincheloe and Stehn, 1991; Jorgenson, 2000), which foraging geese prefer because of high nutrient content (Sedinger and Raveling, 1984; Laing and Raveling, 1993; Ruess et al., 1997). Grazing pressures on *C. subspathacea* are high (Person et al., 1998), and geese sometimes forage in the adjacent, less nutritious *C. ramenskii* community (Ruess et al., 1997). If intensively grazed, *C. ramenskii* is maintained as a form reverts to a form of vegetation that is morphologically and nutritionally similar to *C. subspathacea* (Person et al., 2003). In this paper, we use the term grazing lawn to refer to *C. subspathacea* and *C. ramenskii* that has reverted to a form indistinguishable from *C. subspathacea*. Other dominant communities in this region include slough-levee consisting of *Arctophila fulva*, *C. lyngbyaei*, *Deschampsia caespitosa, Elymus arenarius, Poa arctica,* and *Triglochin palustris*, and uplands of *Empetrum nigrum*, *Sphagnum spp*, *Betula nana*, and *Cladina rangiferina* (Kincheloe and Stehn, 1991; Babcock and Ely, 1994; Jorgenson, 2000).

METHODS

Videography Flights

We used aerial videography (Anthony et al., 1995; Person et al., 2003) to sample habitats used by broods of emperor geese (Fig. 1). Flights were conducted prior to hatching of emperor goose eggs in early June of 1999, 2003, and 2004. Information about the distribution of emperor goose broods (Bowman and Larned, 2000; C. Ely, unpubl. data) was used to delineate the six locations sampled, and 5 – 13 transects were flown at each location (Fig. 1). Approximately 16 hours of total flight time was needed to sample all 52 transects.

Two digital cameras (mini-DV format) mounted near the aft bulkhead of a Cessna 206 aircraft recorded vegetation on the ground while flying about 150m above ground level. The cameras were connected to the avionics system of the aircraft for annotating the video by the two-person flight crew. A color monitor received images from the cameras in the aircraft. A GPS receiver linked to a laptop computer recorded the latitude and longitude of the aircraft each second, as well as the transect number, time, and date. When recording of latitude and longitude were not continuous (~13% of the time), we interpolated the latitude and longitude from adjacent locations. In real time, the location of the moving aircraft relative to each transect was displayed on the computer screen. In 1999 and 2004, one camera was set to record a telephoto view (72mm focal length; ~69m^2 on the ground) and the other camera recorded a wide view (16mm focal length; ~1387m^2 on the ground), but in 2003 both cameras were mistakenly set to record a telephoto view. Each year we flew along the same transects, but the vegetation recorded

by the videography was different because of the small coverage of the telephoto view and deviations from the transect caused by wind gusts, precision of GPS locations, and other uncontrollable factors.

Sampling Videography Data

Prior to sampling, we established eight habitat categories that described all of the sampled area. *A priori*, we chose to limit habitats to eight categories with the expectation that this would limit classification error yet still provide meaningful resolution to interpret relations between habitats and consumers. These categories were (1) grazing lawn (*C. subspathacea* and reverted *C. ramenskii*), (2) sedge meadow (primarily *C. ramenskii* and *C. rariflora*), (3) slough-levee (primarily *Elymus arenarius, Poa arctica,* and *Deschampsia caespitosa*), (4) upland (primarily *Empetrum nigrum*, *Sphagnum spp*, and *Betula nana*), (5) mud, (6) pond or lake, (7) river or slough, and (8) other (primarily pieces of driftwood; Kincheloe and Stehn, 1991; Babcock and Ely, 1994; Jorgenson, 2000). While we collected information on all eight categories, we present only percent aerial extent of grazing lawns as this habitat is most relevant to broods of emperor geese (Laing and Raveling, 1993; Schmutz, 2001; Schmutz and Laing, 2002).

After each field season, we displayed the video using two S-video monitors connected to VCRs, which displayed images from both the telephoto and wide view collected in 1999 and 2004, and the telephoto view collected in 2003. We were able to match images from the telephoto and wide views using the time stamp from each one-second frame. This allowed us to simultaneously view the frame from the telephoto view on one monitor and the location of the telephoto frame within the wide view on the other

monitor. We then sampled the videotape by stratifying by transect within each location. We defined the sample unit as a one-second frame of the videotape, and we randomly chose 150 – 160 one-second frames within each location, each separated by a minimum of 200m. For each selected frame, we overlaid a coverage of 180 systematically distributed dots onto the telephoto view monitor and visually assigned each dot to one of the eight habitat categories. The percent extent of grazing lawns was the proportion of these 180 dots that were classified as grazing lawn. In addition, using the wide view from 1999 and 2004 we assigned collections of dots classified as grazing lawn as being either adjacent to a pond or river.

Grazing lawns are distributed around river corridors (Kincheloe and Stehn, 1991), and transects were generally oriented parallel to rivers (Fig. 1). However, rivers on the Yukon-Kuskokwim Delta frequently alter course, and because of the inability of the plane to follow this course, we potentially sampled habitat outside of the distribution of grazing lawns. Consequently, we were concerned that raw estimates of grazing lawn extent might be biased low, and that the magnitude of this bias might vary among locations, according to the variable juxtaposition of transects to rivers. To correct for this potential source of bias, we made an *ad hoc* adjustment to our data. We first calculated the distance from each grazing lawn to the nearest river edge. For each location, we then determined the maximum distance of sampled grazing lawns to rivers. We truncated data for each location at that distance, and excluded observations beyond the maximum distance, which resulted in different numbers of frames among locations and years being included in our analyses of grazing lawn extent (Table 1).

Ground Truthing

We conducted ground truthing in 2003 and 2004 to assess how accurately we classified habitats with the videography. In 2003, prior to the videography flight, we randomly placed five, 1km long transects on the ground within the Manokinak River location. Along each transect, we placed five large white markers on the ground in the form of an "X" about every 200m. The aircraft flew over these transects, recording the vegetation below. However, because of the difficulty of maintaining the aircraft in a straight line, the number of markers that were captured on the videotape was reduced from 25 to 18. From the videography, we printed color images that displayed the markers and surrounding habitat. We returned to the field about three weeks later with these images, and after locating each marker, classified habitat on the corresponding image.

We used different methodology in 2004 to expand our ground truthing efforts to another location. After the videography was conducted and we had sampled the videotape, we randomly selected 75 of the previously sampled frames from Manokinak River and Old Chevak (150 total) to locate on the ground. We created a color paper printout of each frame that contained both the telephoto and wide views and the corresponding coordinates for the second during which both frames were taken. We used handheld GPS receivers to locate each frame's general area on the ground. We then used the corresponding wide view to match pond, meadow, and river configurations, which allowed us to align ourselves and locate the vegetation on the ground which matched that on the telephoto view. For many frames, it was not possible to find the telephoto view

within the wide view, and so we omitted these frames, which reduced our sample size to 21 at Manokinak River and 16 at Old Chevak. Once located, we classified habitats observed directly on the ground to compare with our independent classification of these same habitats as observed from the videography frame. For both ground and videography-based classification, multiple categories of habitat often occurred within a single frame. When that happened, observers delineated breaks in habitat type and classified the different types.

Data Analysis – Ground Truthing

We used producer's and user's accuracies, standard statistics in remote sensing applications (Congalton, 1991; Verbyla, 1995; Foody, 2002), to estimate the accuracy at which we classified grazing lawn and non-grazing lawn habitat from the videography. User's accuracy reflects how often a given habitat (e.g., grazing lawn) that is detected on the ground is accurately classified as grazing lawn on the videotape. Producer's accuracy reflects the proportion of all videography-based classifications of a given habitat (e.g., grazing lawn) that are in fact that habitat, as evaluated from ground-based observations. User's and producer's accuracy are reported as percentages, with a measure of 100% indicating no error. Use of producer's and user's accuracy requires three assumptions be fulfilled (Verbyla, 1995): (1) the ground truthing data are representative of the entire classification, (2) the ground truthing data and classified frame are perfectly co-registered, and (3) there are no errors in the ground truthing data. We believe we met these assumptions. Although we were unable to conduct ground truthing at four videography locations, the Manokinak River and Old Chevak locations were

representative of the range of habitat types among all locations. Old Chevak is the most inland and elevated location, whereas Manokinak River is more coastal and similar in habitat features and topography to the other locations sampled (Kincheloe and Stehn, 1991). We were unable to locate many of the randomly selected ground truthing points in 2004 and some in 2003. Most points were omitted because they lacked sufficient pond, meadow, or river signatures to enable their location. Nevertheless, we believed that the ground truthing points included were representative of the surrounding habitat as habitat types occurred in nearly equal proportions between the ground truthing and videography data. Our data were perfectly co-registered because we were able to locate, on the ground, the frames we sampled on the videography. We minimized the potential for error in the ground truthing data by training observers in identification of habitat types. If some observers were unsure of habitat type, they collected detailed notes on vegetation characteristics, and habitat type was later classified by the first or third author.

Data Analysis – Model Selection and Parameter Estimation

For each analysis, we created a set of candidate models that represented different hypotheses about variation in grazing lawn extent. We used an information-theoretic approach (Burnham and Anderson 1998) to evaluate the relative support for the models we proposed to address our hypotheses. We used Proc GLM (SAS Institute, 2001) to generate estimates of grazing lawn extent and evaluate the relative support for our candidate models. Because our response variable was a proportion, we applied arcsine transformations to grazing lawn extent prior to analysis to better meet distributional assumptions of linear models (Sokal and Rohlf, 1995). Relative differences in Akaike's

Information Criterion (ΔAIC), or Akaike's Information Criterion, corrected for finite sample size (ΔAIC_c) were used to discriminate among competing models (Burnham and Anderson, 1998). We used summed Akaike weights to quantify the level of support for individual variables. Whenever necessary, we interpreted beta coefficients and their associated confidence intervals. We computed back-transformed, least-squares estimates of grazing lawn extent from the best approximating model in each analysis.

We conducted two analyses of variation in grazing lawn extent. The first analysis examined variation among years and locations, and included data from Aknerkochik River, Kokechik Bay, Manokinak River, Old Chevak, and Opagayarak River in 1999, 2003, and 2004, and Naskonat Peninsula in 1999 and 2003 (Table 1). We were only able to collect information on the adjacency of grazing lawns to ponds and rivers in 1999 and 2004. Thus, we restricted the analysis of variation within locations to 1999 and 2004, and we excluded Naskonat Peninsula, which was not surveyed in 2004.

For the analysis among years and locations, we included ten models, which represented variation in grazing lawn extent as a function of some combination of the variables year, trend in year, location, and Kokechik Bay separate from the other five locations. Among years, the extent of grazing lawns is dynamic and Person et al. (2003) documented an increase during a period in which the population size of black brant was increasing. They reported that while the extent of grazing lawns was related to goose density, it was best described by a four-year time lag. Population size of emperor geese has not exhibited significant change since 1985, and since 1996, population size of cackling geese, the more numerically dominant species in locations we sampled, has been

relatively stable (Eldridge, 2003). Numbers of black brant at Kokechik Bay have been steadily declining since 2000 (Anthony, 2004). Thus, we predicted that grazing lawn extent in our study would be stable or perhaps declining during 1990 – 2004. We had reason to suspect a decline in grazing lawn extent because of recent years of low nest success (Fischer et al., 2004), which significantly reduced the numbers of broods needed for maintaining grazing lawns. Among locations, we predicted that grazing lawn extent could differ from variation in grazing intensity (or past history of grazing) or edaphic and topographic conditions (Ruess et al., 1997). We also included a model with transect nested within location to examine whether extent of grazing lawns was more variable within- than among- locations in this analysis. Because Kokechik Bay contains a black brant colony (Anthony, 2004), coupled with comparatively similar numbers of cackling and emperor geese, we predicted that patterns of variation in grazing lawn extent may differ between Kokechik Bay and the other five locations.

For the analysis within locations, we included 11 models, which represented variation in grazing lawn extent as a function of some combination of the variables location, year, and pond/river. Year and location were included because of afore-mentioned reasons. We predicted greater extent of grazing lawns adjacent to ponds versus rivers because of a hypothesized form of *C. ramenskii* that occurs further inland and exhibits a more plastic response to grazing; hence it is more easily reverted (Person, 2001). In both analyses, we considered models which included additive effects and interactions among variables. All variables included were categorical except trend in year, which was continuous.

RESULTS

We estimated producer's and user's accuracy from 18, 21, and 16 frames sampled on the ground at Manokinak River in 2003, Manokinak River in 2004, and Old Chevak in 2004, respectively. We analyzed variation among years and locations from 2441 frames sampled at five locations in 1999, 2003, and 2004 and one location in 1999 and 2003. To assess variation within locations, we analyzed 1429 frames sampled at five locations in 1999 and 2004. The percentage of videotape sampled varied among locations and ranged from 4 – 12 percent within a year (Table 1).

Detection of Grazing Lawn

Producers accuracy for grazing lawn ranged from 97.5% to 100% and user's accuracy ranged from 91.6% to 98.7% (Table 2). Non-grazing lawn ranged from 99.7% to 99.9% and 99.8% to 100% for producer's and user's accuracy, respectively. There was a small annual difference (range 0.2% – 7.1%) in producer's and user's accuracy for grazing lawn and non-grazing lawn at Manokinak River in 2003 and 2004 (Table 2). Similarly, there was a small spatial difference (range 0.1% – 2.5%) in producer's and user's accuracy for grazing lawn and non-grazing lawn in 2004 at Manokinak River and Old Chevak.

Variation Among Years and Locations

The best approximating model indicated that grazing lawn extent varied among locations, but not years (Table 3). There was some support for a model incorporating a trend in year (ΔAIC = 1.80), although the trend coefficient was not distinguishable from zero (β_{YEAR} = -0.0006, SE = 0.001). Consistent with our prediction, grazing lawn extent

was stable or may have declined slightly during 1999 – 2004. Mean estimates (± SE) of extent varied from 1.8 (0.7) – 7 (0.7) percent among locations, and were highest at Kokechik Bay and lowest at Manokinak River (Fig. 2). Aknerkochik River and Naskonat Peninsula had similar, but greater extent of grazing lawns than did Old Chevak and Opagayarak River, which were also similar (Fig. 2). Models with Kokechik Bay separate from all other locations received little support ($\Delta AIC \geq 9.79$), as did a model with no variation ($\Delta AIC = 27.41$), and a model with transect nested within location ($\Delta AIC = 30.93$; Table 3).

Variation Within Locations

Grazing lawn extent varied with adjacency to a pond or river, as the best approximating model contained additive effects of both location and pond/river (Table 4). Consistent with our prediction, grazing lawn extent was greater adjacent to ponds than rivers (difference = 0.04, SE = 0.01). Among locations, mean estimates (± SE) of grazing lawn extent adjacent to ponds varied from 3.5 (0.9) – 8.3 (0.9) percent, and adjacent to rivers varied from 0.0 (1.0) – 4.7 (1.0) percent (Fig. 3). A model with similar structure to the best approximating model, but including a parameter for year, received limited support ($\Delta AICc = 2.02$). However, the addition of a parameter for year resulted in no improvement to model fit, and the $\Delta AICc$ of 2.02 was largely the result of the penalty for adding this parameter (Anderson and Burnham, 2002).

DISCUSSION

Utility of Aerial Videography

Aerial videography is a useful method to sample a large region quickly and accurately identify fine-scale, patchily-distributed habitats. A study with similar objectives to ours but using just ground-based sampling took two weeks to cover one-third of the area we sampled (Kincheloe and Stehn, 1991). Another study (Jano et al., 1998) used satellite imagery to sample habitats used by lesser snow geese (*Anser caerulescens caerulescens*) across a large scale, but was only able to discern vegetation from non-vegetation, and could not identify grazing lawns used by broods of that species. Our videography method combined quick, relatively inexpensive sampling with the ability to identify fine-scale habitat patches, such as grazing lawns, across large spatial extents. Further, these capabilities increase its applicability to other ecosystems where the effects of land use and climate change are expected to alter land cover (Dale, 1997).

Using aerial videography, we were able to classify grazing lawn and non-grazing lawn habitat with a high degree of accuracy. Thomlinson et al. (1999) suggested a minimum criteria for land cover classification of 70% accuracy per category and 85% accuracy overall. Our efforts produced results that exceeded those criteria for both grazing lawn and non-grazing lawn. Most misclassified values were small patches of grazing lawn that were overlooked while sampling the videography frames.

Temporal differences in accuracy may have been due to variation among years in weather or lighting conditions, or phenology of green-up. Nevertheless, accurate

identification of habitat types was still possible. Under similar videography conditions, Anthony et al. (1995) reported that even under poor weather and lighting conditions, precise estimation of brant populations was possible with videography. Spatial differences in identification of grazing lawn and non-grazing lawn habitat were minimal. Overall, high accuracy of detecting grazing lawns was likely related to their comparatively short growth form.

Patterns of Variation in Grazing Lawn Extent

We detected no temporal change or a slight decline in the extent of grazing lawns, among- and within- locations. Ruess et al. (1997) suggested that grazing by geese in grazing lawns and the adjacent *C. ramenskii* vegetation exerts strong influence on the dynamics of the grazing lawn community. During a period of increase in the herbivore population (black brant), Person et al. (2003) documented an increase in grazing lawn extent, which they attributed to reversion of *C. ramenskii* from increased grazing intensity by black brant. We suspect that temporal stability in the extent of grazing lawns during the years of our study may have been due to the relatively constant population size of cackling and emperor geese. We also did not detect temporal variation in grazing lawn extent when Kokechik Bay, which contained a black brant colony, was contrasted with the other sampled locations.

Recent years of low nest success (Fischer et al., 2004) may explain the slight decline we observed in grazing lawn extent. Arctic foxes (*Alopex lagopus*) are the primary predator of nests on the Yukon-Kuskokwim Delta (Thompson and Raveling, 1987), in some years causing nearly complete nesting failure of some goose populations

(Anthony, 2004; Fischer et al., 2004). Since 2000, incidences of fox predation have been greater than those observed during the previous 15 years, with relatively few or no broods produced in 2001 and 2003 (Fischer et al., 2004; Anthony, 2004). The shift in grazing lawns is bi-directional (Ruess et al., 1997; Person et al., 2003). In other words, geese need to maintain constant grazing pressure on grazing lawns or they may revert back to a state similar to the less nutritious *C. ramenskii*. Consequently, intensive fox predation in some years may have led to sufficient reductions in grazing pressure to cause large-scale loss in the extent of grazing lawns. We suspect that such significant reductions in grazing pressures may also accelerate the time lag of four years reported by Person et al. (2003).

Among locations, we detected a substantial amount of variation in grazing lawn extent. Variation in topography and edaphic characteristics could have contributed to these location-specific differences; however, grazing by geese exerts the strongest influence on dynamics among *Carex* species within a community (Ruess et al., 1997). Nonetheless, we are unsure of the underlying reasons for such large variation among locations, as patterns of variation in densities of herbivores are similar across many sampled locations (B. Lake unpubl. data).

Within locations, grazing lawn extent was 4% higher adjacent to ponds than rivers, and some locations contained <2% grazing lawn extent adjacent to rivers. Schmutz (2001) reported that selection of habitats by broods of emperor geese was strongest for saline pond and lower for mudflats bordering rivers. Unlike Schmutz's (2001) conjecture of what habitats were used for foraging, our results suggest that emperor geese may have selected these pond habitats due to greater forage availability.

This result could also be an artifact of past selection for saline ponds, which resulted in increased grazing lawn extent through the reversion process (Person et al., 2003). In response to mammalian predators, broods of emperor geese commonly move onto mudflats or rivers (Laing and Raveling, 1993). Given the difference in grazing lawn extent adjacent to ponds versus rivers, broods likely face trade-offs between minimizing risk of predation and maximizing the amount of available forage.

The greater extent of grazing lawns adjacent to ponds than rivers has important implications for land-cover change. In Arctic ecosystems, change in the amount of ponds and lakes has been most pronounced (Stow et al., 2004). Although Person and Ruess (2003) documented that grazing lawns were tolerant of increased salinity, knowledge of the response to declines in salinity and soil moisture from pond recession is of great importance. Observations during the summers of 2003 and 2004 suggested that pond water levels declined causing some minor loss of grazing lawn habitat (B. Lake, pers. observation) and we suggest that future declines could have significant impact on the extent of grazing lawns adjacent to ponds.

Relevance to Population Dynamics and Management

Grazing by geese influences and often mediates patterns of forage quantity and quality (Bazely and Jefferies, 1985; Ruess et al., 1989; Hik and Jefferies, 1990; Mulder and Ruess, 1998; Person et al., 2003), which in turn affects the geese themselves. For example, body mass of goslings is strongly associated with variation in the quantity and quality of forage (Cooch et al., 1991; Sedinger and Flint, 1991; Cooch et al., 1993), including the extent of grazing lawns (Person et al. 2003). Consequently, the large-scale

variation in grazing lawn extent we detected likely contributes to variation in the body mass emperor geese achieve prior to fledging. Because larger emperor goslings survive at a higher rate (Schmutz, 1993), such a result has implications the dynamics of this population.

Our study sampled a relatively large proportion of the habitat used by emperor geese during brood rearing. Productivity of this species declined during 1996 – 2003 (Anderson et al, 2003), possibly from negative density-dependent effects on body mass of goslings (Schmutz and Laing, 2002). Our results indicate that grazing lawn extent has not changed, and may have slightly declined, during a period of relative population stability across the composite goose community. We suggest that management to increase the population size of emperor geese should include consideration of density-dependent effects on body mass and survival. For instance, the United States Fish and Wildlife Service has proposed to conduct wide-scale glaucous gull (*Larus hyperboreus*) removal to increase gosling survival and recruitment (Bowman et al., 2004). Without consideration of density-dependent effects (Schmutz and Laing, 2002), such a control effort may actually increase competition, thereby reducing body mass and post-fledging survival of that cohort (Schmutz, 1993), and offsetting some of the benefits of improved gosling survival. However, one possibility is that after a lag of several years, this increased competition may ultimately promote increased amounts of grazing lawn and thus higher carrying capacities (Person et al., 2003). Clearly, the prospect for both negative (Schmutz and Laing, 2002) and positive (Person et al., 2003) effects of geese on the biomass and extent of their preferred food plants creates complexity in understanding

ecosystem processes and hinders informed management and conservation. To elucidate these complex processes, landscape-level monitoring of both the consumers and the food resources is needed. Our videography technique provides that opportunity for the food resource, which until now has not been examined at such a scale.

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TABLE 1. Numbers of frames included in analysis of variation in grazing lawn extent among years and locations. For the analysis of grazing lawn extent within locations, we included all frames except those from 2003 and Naskonat Peninsula. Values in parentheses indicate percentage of videotape sampled.

Year	Aknerkochik River	Kokechik Bay	Manokinak River	Naskonat Peninsula	Old Chevak	Opagayarak River	Total
1999	152 (7%)	148 (4%)	147 (4%)	149 (12%)	136 (5%)	139 (5.5%)	871
2003	151 (8%)	142 (4%)	148 (5%)	147 (12%)	135 (5%)	140 (5.5%)	863
2004	149 (7%)	143 (5%)	142 (4%)	0	132 (4%)	141 (4.5%)	707
Total	452	433	437	296	403	420	2,441

TABLE 2. Producer's and user's accuracy for classification of grazing lawn and non-grazing lawn habitat. Producer's accuracy reflects the error in values omitted from a category that should have been included. User's accuracy reflects error from values incorrectly classified. User's and producer's accuracy are reported as percentages, with a measure of 100% indicating no error.

Location – Year	Producer's Accuracy		User's Accuracy		Overall
	Grazing Lawn	Non-Grazing Lawn	Grazing Lawn	Non-Grazing Lawn	
Manokinak River – 2003	100	99.7	91.6	100	99.8
Manokinak River – 2004	97.5	99.9	98.7	99.8	99.8
Old Chevak – 2004	100	99.8	96.8	100	99.8
Annual Difference[1]	2.5	0.2	7.1	0.2	---
Spatial Difference[2]	2.5	0.1	1.9	0.2	---

[1]Difference between Manokinak River in 2003 and 2004

[2]Difference between Manokinak River in 2004 and Old Chevak in 2004

TABLE 3. Candidate models for investigation of variation in grazing lawn extent among years and locations. Estimates are based on sampling conducted at Aknerkochik River, Kokechik Bay, Manokinak River, Old Chevak, and Opagyarak River in 1999, 2003, and 2004, and Naskonat Peninsula in 1999 and 2003. Models are ranked by relative differences in AIC values.

Model[1]	K[2]	Log(L)[3]	ΔAIC	w[4]
Location	7	4192.93	0.00	0.68
Location + YEAR[5]	8	4193.01	1.80	0.28
Location + Year	10	4193.11	5.58	0.04
Kokechik Bay, All Other Locations	3	4185.20	9.79	0.00
Kokechik Bay, All Other Locations + Year	6	4185.49	15.12	0.00
Kokechik Bay, All Other Locations * Year	7	4185.97	16.01	0.00
Location * Year	18	4194.55	18.27	0.00
Null	2	4176.68	27.41	0.00
Year	4	4176.92	30.87	0.00
Transect (Location)	53	4219.45	30.93	0.00

[1]The "+" between variables indicates an additive effect; the "*" denotes an interaction; the "( )" denotes a nested effect

[2]Number of parameters

[3]Maximized log-likelihood

[4]Weight of evidence for being the best approximating model for each group

[5]Linear time trend

TABLE 4. Candidate models for investigation of variation in grazing lawn extent within locations. Estimates are based on sampling conducted at Aknerkochik River, Kokechik Bay, Manokinak River, Old Chevak, and Opagyarak River in 1999 and 2004. Models are ranked by relative differences in AIC*c* values.

Model[1]	K[2]	Log(L)[3]	ΔAIC*c*	w[4]
Location + Pond/River	7	2371.30	0.00	0.72
Location + Year + Pond/River	8	2371.30	2.02	0.26
Location * Pond/River	11	2371.57	7.49	0.02
Year + Pond/River	4	2363.20	12.61	0.00
Year * Pond/River	5	2363.77	13.30	0.00
Location	6	2363.28	16.45	0.00
Location + Year	7	2363.30	18.42	0.00
Location * Year * Pond/River	21	2375.59	18.69	0.00
Location * Year	11	2364.43	23.92	0.00
Null	2	2355.36	26.62	0.00
Year	3	2355.39	28.58	0.00

[1]The "+" between variables indicates an additive effect; the "*" denotes an interaction

[2]Number of parameters

[3]Maximized log-likelihood

[4]Weight of evidence for being the best approximating model for each group

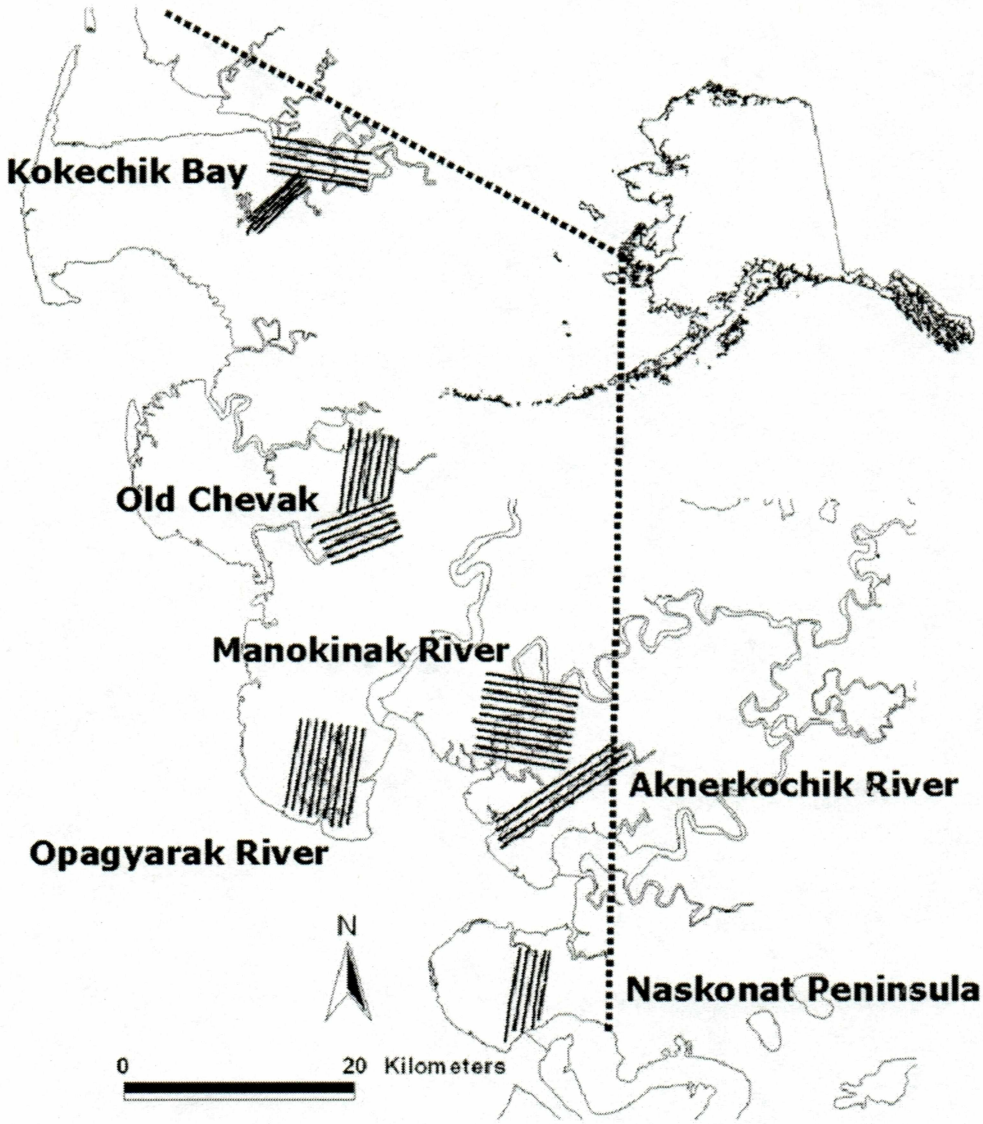

FIG. 1. Distribution of videography transects across the Yukon-Kuskokwim Delta, Alaska. Aknerkochik River, Kokechik Bay, Manokinak River, Old Chevak, and Opagyarak River were sampled in 1999, 2003, and 2004, and Naskonat Peninsula was sampled in 1999 and 2003.

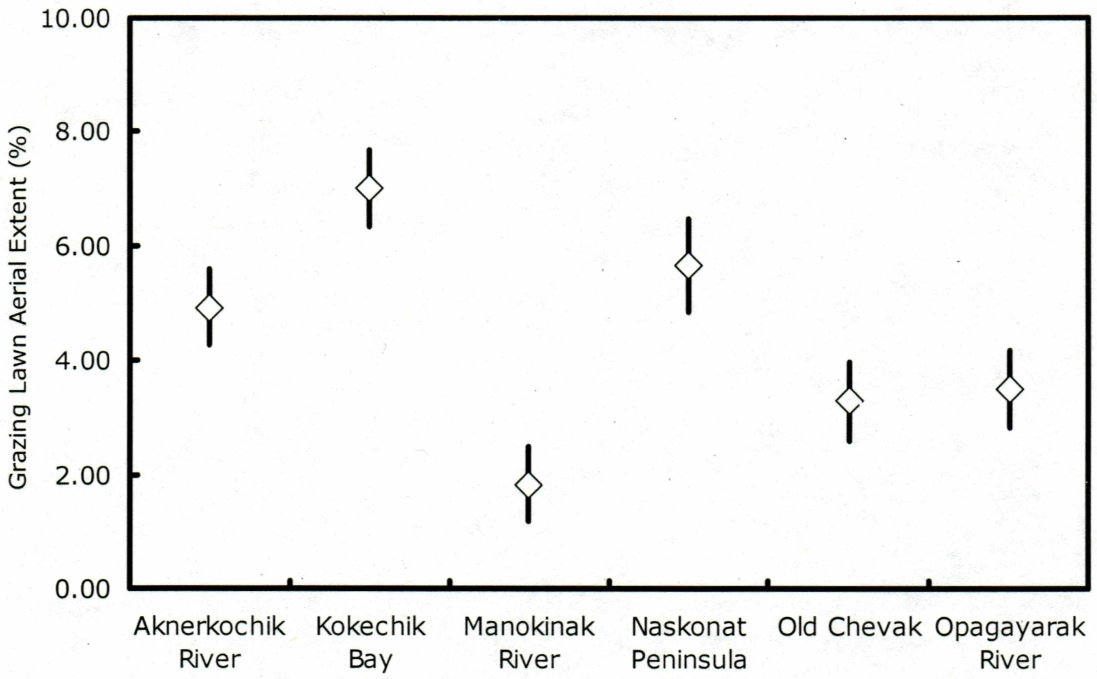

FIG. 2. Aerial extent of grazing lawns ($\overline{X} \pm SE$) at six locations used by broods of emperor geese. The best approximating model included an effect of location, but did not include year (1999, 2003, and 2004).

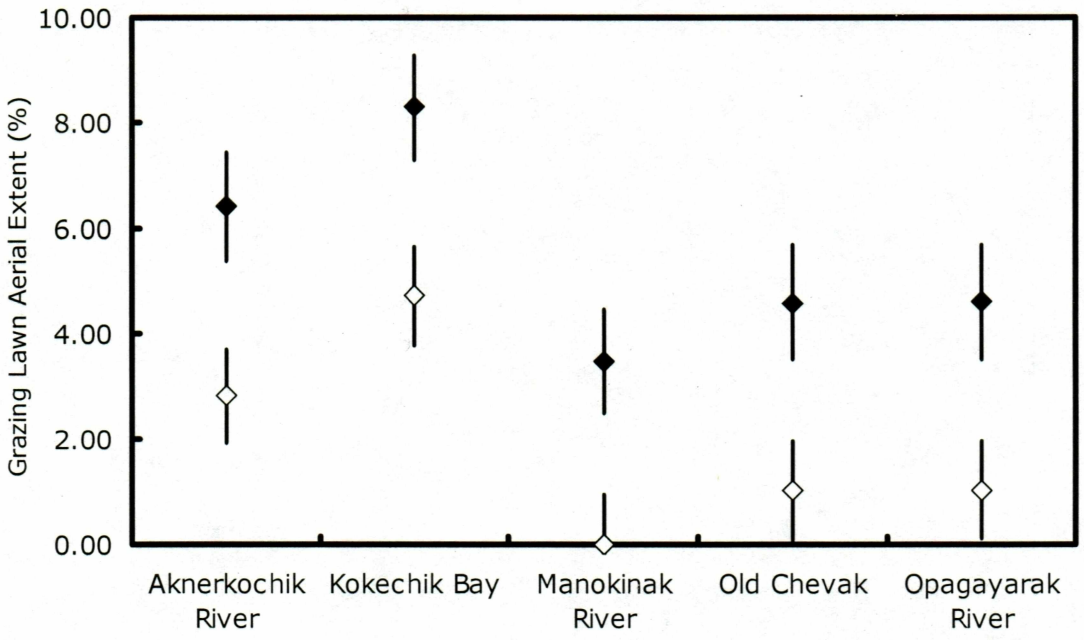

FIG. 3. Aerial extent of grazing lawns ($\overline{X} \pm SE$) adjacent to ponds (closed diamonds) and rivers (open diamonds). The best approximating model included an additive effect of location and pond/river, but did not include year (1999 and 2004).

Spatial and temporal variation in body mass of prefledging Emperor Geese: Effects of interspecific goose densities and grazing lawn extent[1]

Abstract.—Growth of juvenile arctic and sub-arctic nesting geese is strongly linked to forage quantity and quality, which are mediated by densities of geese using the forage. We studied variation in body mass of prefledging Emperor Geese (*Chen canagica*) at three locations across the Yukon-Kuskokwim Delta, Alaska during 1990 – 2004 to investigate whether body mass was related to interspecific competition for forage. From 1990 – 2004, densities of Cackling Geese (*Branta hutchinsii*) more than doubled and were ~2 – 5x higher than densities of Emperor Geese, which were relatively constant over time. During 2003 – 2004, body mass of prefledging Emperor Geese varied among locations and between years, increased with grazing lawn extent and net above-ground primary productivity (NAPP), and declined with interspecific goose densities (Cackling and Emperor Geese). In those same years, grazing by geese resulted in consumption of ≥ 90% of the NAPP that occurred in grazing lawns during the brood rearing period, suggesting that interspecific competition was from exploitation of common food resources. Because we sampled at multiple sites representing a range of densities and forage availability, we suggest that such competition is broadly relevant across the Yukon-Kuskokwim Delta, the primary breeding area for this species. Productivity of Emperor Geese, as measured in fall surveys, declined the last eight years, as compared to

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[1]Prepared for *Auk* as Lake, B. C., J. A. Schmutz, M. S. Lindberg, C. R. Ely, W. D. Eldridge, and F. J. Broerman. Spatial and temporal variation in body mass of prefledging Emperor Geese: Effects of interspecific goose densities and grazing lawn extent.

the previous eleven. We suggest that this decline may be influenced by negative effects of interspecific goose densities on prefledging body mass because of a positive correlation between body mass and survival to fall staging areas (Schmutz 1993). Management to increase the population size of Emperor Geese should consider interspecific densities of geese and their interactions with forage.

INTRODUCTION

Early growth of arctic and sub-arctic nesting geese has important consequences for fitness. Growing seasons in arctic regions are short, and goslings must acquire sufficient nutrients for growth and fledging prior to migration (Herzog and Sedinger 2004). In response to such selective pressures, geese have evolved rapid growth relative to other precocial species of similar size (Sedinger 1992). Such rapid growth, however, increases the importance of food resources, which are often limited (Sedinger and Raveling 1984, Larsson and Forslund 1991, Williams et al. 1993). Consequently, substantial variation exists in the body mass goslings achieve prior to fledging (Cooch et al. 1991a, b, Lepage et al. 1998, Herzog 2002). In addition, spatial and temporal variation in body mass makes significant contributions to population dynamics of geese because larger goslings survive at a higher rate during their first year (Schmutz 1993, Van Der Jeugd and Larsson 1998, Cooch 2002) and have higher breeding probability (Sedinger et al. 2004) and fecundity as adults (Sedinger et al. 1995).

Growth is particularly sensitive to the per capita availability of high-quality forage (Cooch et al. 1991a, b, Sedinger and Flint 1991, Sedinger et al. 1998), which is mediated by densities of geese using the forage (Cargill and Jefferies 1984, Gauthier et

al. 1995, Person et al. 1998). Previous researchers have examined intraspecific effects of geese on body mass (Cooch et al. 1991b, Sedinger et al. 1998); however, few studies (Schmutz and Laing 2002) have examined how interspecific competition affects patterns of variation in body mass of prefledging geese.

Three pieces of evidence suggest that interspecific competition is relevant to prefledging Emperor Geese (*Chen canagica*). First, broods of Emperor Geese strongly select grazing lawns of *Carex subspathacea* (Laing and Raveling 1993, Schmutz 2001), which are shared with Cackling Geese (*Branta hutchinsii*) and Black Brant (*B. bernicla nigricans*; Schmutz and Laing 2002). Such overlap occurs despite preference for other habitats by Cackling Geese (Sedinger and Raveling 1984, Schmutz 2001) and use of other habitats by Black Brant (Mulder and Ruess 1998). Second, vegetation in grazing lawns is heavily exploited, implying a limitation. Each summer, geese consume up to 95% of the net above-ground primary productivity (NAPP; Person et al. 1998, Person and Ruess 2003). Furthermore, the extent of these grazing lawns is dynamic, in part due to interactions with consumers, and the percent aerial coverage has strong influence on the body mass of goslings (Person et al. 2003). Finally, research conducted during 1993 - 1996 invoked interspecific competition by demonstrating that time spent foraging and body mass of Emperor Goose goslings were more strongly related to the collective density of Black Brant, Cackling Geese, and Emperor Geese than to the density of Emperor Geese alone (Schmutz and Laing 2002).

However, that research was conducted at just a single study site, and because goose density varies across the Yukon-Kuskokwim Delta (U.S. Fish and Wildlife Service

unpubl. data), its population-level relevance to Emperor Geese was unresolved. Because Cackling Geese have more than doubled in population size since 1990 (Eldridge 2003), we expected that interspecific competition may be relevant at a larger scale. Elucidating whether interspecific competition affects body mass of prefledging Emperor Geese across the Yukon-Kuskokwim Delta is important because it would be expected to influence, due to the relationship between body mass and survival (Schmutz 1993), the proportion of young observed during fall surveys (the fall age ratio). Fall age ratios are measured at migratory staging areas during late September from photo surveys of nearly the entire population of Emperor Geese, and this measure of productivity declined an average of 39% during the period 1996 - 2003 as compared to 1985 – 1995 (Anderson et al. 2003).

Our objective was to address whether inter-specific competition for food is relevant to prefledging Emperor Geese at a population level by conducting a study at multiple locations across the primary breeding range of this species. We investigated the hypothesis that body mass was a function of per capita food availability, and during 2003 and 2004, we conducted sampling at three locations that reflected two high goose density areas and one low goose density area and were distributed across the Yukon-Kuskokwim Delta. At each location in each year, we estimated species-specific goose densities (Emperor and Cackling Geese), and we also estimated food availability. Food availability was represented by net above-ground primary productivity (NAPP) and spatial extent of *C. subspathacea* grazing lawns, variables not included in the analysis of Schmutz and Laing (2002). Extent of grazing lawns was measured with aerial videography (Person et al. 2003, Chapter 1). We also examined the hypothesis that

longer-term variation in body mass (1990-2004) was related to goose densities, although measures of food availability were not obtained in all years. From these results, we suggest that increasing interspecific competition, through its effect on juvenile body mass and survival, has contributed to the decline in the fall age ratio of Emperor Geese.

STUDY AREA AND METHODS

We studied variation in body mass of prefledging Emperor Geese at Kokechik Bay (62°N, 166°W), Old Chevak (61.5°N, 165.5°W), and Manokinak River (61°N, 165°W). These locations are distributed along the coastal fringe of the Yukon-Kuskokwim Delta, Alaska, and are within 5km of the Bering Sea, except Old Chevak (13km). Previous research at these locations suggested that broods of Emperor Geese strongly select the grazing lawn community for foraging (Laing and Raveling 1993, Schmutz 2001, J. Schmutz unpubl. data). This community occurs at the interface of *C. ramenskii* meadows, along riparian mudflats and pond margins, and is comprised primarily of *C. subspathacea*. Other major communities used by broods of Emperor Geese include sedge meadow, comprised primarily of *C. ramenskii* and *C. rariflora* (Schmutz 2001), and slough-levee, containing *Triglochin palustris* (Laing and Raveling 1993).

Estimating densities of nesting geese.—Aerial surveys to estimate the abundance of all four species of nesting geese have been conducted since 1985 on the Yukon-Kuskokwim Delta. Survey methods were described in detail in Butler et al. (1995). Briefly, each year a sample of transects (~ 24km length) that covered the Yukon-Kuskokwim Delta were randomly selected and surveyed. Starting in 1998, the same

randomly selected transects were sampled on a four-year rotation. Transects were oriented East-West, and were 1.6km apart in high goose density areas, and 12.8 km apart in low goose density areas. The pilot and observer recorded observations up to 200m on each side of the aircraft, and the location of each observation was recorded with LORAN-C or GPS. Species was recorded for each observation of single and paired geese.

We used survey data of single and paired geese to estimate densities at Kokechik Bay, Manokinak River, and Old Chevak from 1990 – 2004. Information about the distribution of Emperor Goose broods (Bowman and Larned 2000, C. Ely unpubl. data) was used to delineate the three locations. Following Eldridge (2003), we estimated density of nesting geese as 2 * (number of single observations + number of paired observations) divided by the area sampled on each transect (200m on each side of the aircraft * transect length). The ratio estimator we used for estimating density (Williams et al. 2002) assumed that the intercept passed through zero, which was reasonable for Emperor and Cackling Geese because numbers of observations increased with area sampled. However, the clumped and patchy distribution of Black Brant led to violation of this assumption. Consequently, we do not present estimates from Black Brant, although survey data limited to colonies indicates that numbers are fewer than Cackling Geese and similar to Emperor Geese (Anthony 2004). We used means and 95% confidence intervals (Johnson 1999) to make relative comparisons in density among locations and years.

We assumed that densities of nesting geese reflected relative differences in densities of broods among years and locations, given annual rates of nest success. This

assumption was reasonable because the evidence to date suggests little, wide-spread movements of Emperor and Cackling Geese away from nesting locations (J. Schmutz unpubl. data). In contrast, colonially nesting Black Brant do sometimes move long distances to brood rearing areas (Lindberg and Sedinger 1998); however, we did not observe large movements of Black Brant broods into locations we sampled (B. Lake pers. obs.).

Net above-ground primary productivity and apparent offtake in grazing lawns.— We conducted a grazing experiment during the brood rearing period in 2003 and 2004 to estimate NAPP (biomass of fenced, ungrazed vegetation) and apparent offtake (difference between NAPP and vegetation that was grazed; Person et al. 1998) in grazing lawns. Within each location, we established two transects placed parallel to river corridors, and along each we placed six circular wire mesh fences about 50m apart. Fences were deployed during hatch of goslings on 17 June in 2003 and 10 June in 2004, and we removed an initial 10cm x 10cm sample of vegetation adjacent to each fence on those respective dates. Each fence represented two treatments: (1) vegetation that was ungrazed (fenced) and (2) adjacent vegetation that was available to be grazed (unfenced). Just prior to goslings attaining flight capability, we removed a 10cm x 10cm sample of vegetation from each treatment, which occurred on 30 July in 2003 and 27 July in 2004. We collected a total of 36 samples from each location. Because of some disturbance to wire fences, sample sizes were reduced to 33, 30, and 33 at Kokechik Bay in 2003, and Old Chevak in 2003 and 2004, respectively. We removed all above-ground biomass and

dried samples within 24 hours of collection. Later, samples were re-dried at 60°C to a constant weight, and the mass of each sample was recorded (±0.01 g).

We used NAPP as a predictor variable in examining variation in body mass because it provided a measure of the amount of biomass available to be consumed by geese. Apparent offtake (Person et al. 1998) represented the amount of biomass consumed by geese during the brood rearing period (Sedinger et al. 2001) and provided a measure of grazing intensity. It is termed apparent offtake because it may over- or under-estimate actual offtake (McNaughton et al. 1996) from an optimization process with grazers (Hik and Jefferies 1990).

We examined location and year variation in apparent offtake using the mixed models procedure in SAS (SAS Institute 2001, Littell et al. 2002). We included a model for an additive relationship as well as an interaction between the variables. Transect was considered the sample unit and it was included as a random effect. We calculated estimates of apparent offtake from the best approximating model based on Akaike's Information Criterion, adjusted for finite sample size (ΔAIC_c; Burnham and Anderson 1998).

Body mass data.—We captured Emperor Geese during an approximate ten-day period when goslings were about six weeks of age and adults were flightless from wing molt. Because long-distance (> 5km) movements of broods away from nesting locations are rare, and usually occur within five days of hatching, most goslings were reared in the location captured, regardless of where they hatched (J. Schmutz unpubl. data). Goslings were captured during the period 1990 – 2004, but continuous data sets across locations

and years were not collected (Table 1). During hatch at Manokinak River and Old Chevak, a sample of goslings was marked with individually numbered web-tags, which allowed age to be known (±1 d) when recaptured about 40 days later. Mean age of known-age goslings recaptured during 1993 – 1994 and 2002 – 2004 was 42 d (2 SD = 34 – 50). The fledging age for Emperor Geese is about 55 days (Petersen et al. 1994). We recorded body mass of goslings with digital (±1 g; 2002 – 2004) or spring scales (±50 g; 1990 – 1996).

We used data from unmarked goslings to examine sources of variation in body mass during 2003 – 2004 and 1990 – 2004. Ages were not known for unmarked individuals, and we assumed that unmarked goslings hatched on the peak date of hatch at a given location. To estimate peak of hatch, we obtained information on egg development, derived from floating eggs (Westerkov 1950), from a sample of Emperor Goose nests found during random plot searches (Fischer et al. 2004). These searches covered the core nesting area of the Yukon-Kuskokwim Delta every year from 1985 – 2004, except at Kokechik Bay, where they have been conducted occasionally since 1990. Data from years when Kokechik Bay was sampled suggested that peak of hatch occurred one day earlier than at Old Chevak, and we incorporated this difference in our analysis for goslings captured at Kokechik Bay in 2003 and 2004.

Age for unmarked goslings was the difference between peak of hatch at a location and date of capture (Sedinger 1986, Sedinger et al. 1998). While this method of estimating age added sampling error, it should not have added bias because we were just as likely to over- and under- estimate age. Ninth primary length has been used as a

predictor of age (Cooch et al. 1999), but based on analysis of marked, known-age individuals, this method performed poorly for our data. In some years (e.g., 2002) goslings were captured at about 40 days of age, but many individuals had yet to begin growth of their ninth primary.

Previous researchers have documented a seasonal decline in body mass based on an individuals hatch date relative to peak of hatch (Cooch et al. 1991a, Larsson and Forslund 1991, Sedinger and Flint 1991). We believed it was important to control for this source of variation when examining spatial and temporal variation in body mass, and data of marked, known-age individuals from Manokinak River in 1993 – 1994, 2002 – 2004 and Old Chevak in 2003 – 2004 provided the ability to do so.

In all analyses, we calculated a daily growth rate (observed mass/number of days alive) and then adjusted estimates of body mass to 42 days (the mean age of capture of known-age goslings). We assumed that growth of goslings was linear over the range of ages measured, and examination of residuals indicated no significant departures from linear growth.

Model selection and parameter estimation for analyses of variation in body mass.—For each analysis, we created a set of candidate models that represented different hypotheses about variation in body mass. We used an information-theoretic approach (Burnham and Anderson 1998) to evaluate the relative support for the models we proposed to address our hypotheses. We used the mixed model procedure in SAS (SAS Institute 2001, Littell et al. 2002) and maximum-likelihood estimation to evaluate the support for our models and obtain parameter estimates. Relative differences in Akaike's

Information Criterion, adjusted for finite sample size (ΔAIC_c), were used to discriminate among competing models. We used summed Akaike weights to quantify the level of support for individual predictor variables.

We conducted three analyses of body mass. The first analysis investigated variation during 2003 – 2004, and we used a two-step approach in this analysis. In the first step, we investigated more general spatial (location) and temporal (year) variation. We developed a candidate model set of ten models that included the variables location, year, and sex, where the most general model had parameters for each of the six location and year combinations plus a parameter for a constant sex difference. We considered additive relationships as well as interactions between the variables location and year. In the second step, we replaced location and year with ecological variables that we hypothesized could explain the spatial and temporal variation identified in the first step.

Consistent with previous studies (Cooch et al. 1991b, Sedinger et al. 1998, Herzog 2002), we hypothesized that competition for food and, more specifically, per capita food availability may be responsible for much of the spatial and temporal variation observed in body mass. We represented per capita food availability as the estimated densities of geese divided by food availability, where food availability was the product of NAPP (vertical growth of grazing lawn vegetation) and grazing lawn extent (horizontal coverage or extent of grazing lawns; Chapter 1). We predicted that body mass would increase with NAPP and grazing lawn extent (Person et al. 2003) and decline with goose densities (Schmutz and Laing 2002). We included models that reflected interspecific density (combined density of Emperor and Cackling Geese) and contrasted them with

models that only incorporated intraspecific densities (density of Emperor Geese only). The relationship between these variables was body mass = density / (NAPP x extent of grazing lawns). To enable an evaluation of whether density, NAPP, or extent of grazing lawns differed in their individual predictive abilities, we applied a log-transformation prior to analysis, resulting in the following equation: ln(body mass) = ln(goose density) + ln(1/NAPP) + ln(1/extent). We considered additive combinations of these variables and selected among competing models.

We used a single estimate of grazing lawn extent for each location as this measure was similar between 2003 and 2004 (Chapter 1). Because of large annual variation in nest success, which led to substantial variation in the number of broods, we adjusted estimates of density by a species-specific measure of the annual proportion of nests found active during random plot surveys (Fischer et al. 2004). Despite past evidence for the influence of Black Brant densities (Schmutz and Laing 2002), we were unable to consider this species because of afore-mentioned reasons. We used analysis of deviance (ANODEV; Skalski 1996) to calculate the proportion of deviance in body mass from the location by year interaction model explained by the best approximating model incorporating the variables density, NAPP, and grazing lawn extent. The proportion was calculated as (deviance[model incorporating sex]-deviance [model incorporating density, NAPP, grazing lawn extent])/(deviance[model incorporating sex]-deviance[model incorporating location by year]).

The second analysis consisted of known-age (web-tagged) individuals, which allowed us to investigate the effects of relative hatch date on gosling growth and address

whether location and year effects were detectable after controlling for relative hatch date and age. We expected that body mass would decline with hatch date, a result from a limitation in per capita food quality and quantity (Lindholm et al. 1994, Leafloor et al. 1998, Lepage et al. 1998). We included all available data (1993 – 1994, 2002 – 2004 at Manokinak River and 2003 – 2004 at Old Chevak) to increase the statistical power to detect a relative hatch date effect. Twenty-three candidate models were considered; fixed effects included location, year, sex, relative hatch date, and relative hatch date squared. We considered models that included additive effects and interactions between the variables location, year, relative hatch date, and relative hatch date squared. Previous researchers have documented a linear decline in body mass with later hatch date (Cooch et al. 1991a, Sedinger and Flint 1991, Lepage et al. 1998). We predicted that body mass would decline with later hatch date, and we further predicted that this relationship may be quadratic if the seasonal decline in forage is more pronounced after peak of hatch from increased brood densities. We included the identity of the brood as a random effect to account for potential dependence among brood mates. This model structure treated the brood as the sampling unit, which produced a conservative analysis because we sampled only 65 broods.

The third analysis examined whether body mass during 1990 – 2004 exhibited a long-term linear change or was related to annual variation in densities of geese. We considered 16 candidate models in this analysis. Fixed effects were location, sex, trend in year, and years of high and low nest success. Studies have documented the importance of nest success, and by extension, the number of broods in a given year to body mass

(Sedinger et al. 1998, Person et al. 2003). We predicted body mass would be inversely related to nest success, and we categorized nest success as either above or below average (Anthony 2004, Fischer et al. 2004). We considered additive effects and interactions between the variables location, years of high and low nest success, and trend in year. We also considered a model with interspecific densities of geese (combined density of Emperor and Cackling Geese) and a model with intraspecific densities (density of Emperor Geese only), adjusted for annual variation in the proportion of nests found active during random plot surveys (Fischer et al. 2004), to examine whether longer-term variation in body mass was related to goose densities. Year was included as a random effect in all models. By treating year as a random effect we were able to (i) address the variation attributable to year that otherwise would not be explained by the fixed effects with a single parameter (Burnham and White 2002, Link et al. 2002), and (ii) estimate annual process variation in body mass. We used restricted maximum-likelihood estimation to estimate annual process variation in body mass (McCullaugh and Nelder 1989).

RESULTS

We captured 1,387 prefledging Emperor Geese at Kokechik Bay, Manokinak River, and Old Chevak during 1990 – 2004 (Table 1). We recaptured 124 known-age goslings from 65 broods at Manokinak River and Old Chevak (Table 1).

Trends in densities of nesting geese.—Coefficients of variation were large, approaching 35% in some estimates, yet densities of Cackling Geese were variable among locations and years and were ~2 – 5x higher than densities of Emperor Geese

(Table 2). Across locations, estimates of density (mean/km^2, 95% confidence interval) for Cackling Geese more than doubled from 1990 (9.0, 4.8-13.2) to 1996 (19.9, 13.3-26.6) and appeared to be relatively stable from 1996 to 2004 (17.9, 13.7-22.0). Across years, densities of Cackling Geese were lowest at Old Chevak (12.5, 11.1-13.9) and higher but similar between Kokechik Bay (17.8, 15.7-20.0) and Manokinak River (19.6, 17.6-21.7). Densities of Emperor Geese were generally similar among years, except at Kokechik Bay, where densities (mean/km^2, 95% confidence interval) were 2.7 (1.2-4.3) in 1990, 5.5 (4.0-7.1) in 1996, and 7.8 (5.1-10.5) in 2004 (Table 2). Densities of Emperor Geese were lowest at Old Chevak (2.6, 2.3-2.9) and higher, but similar between Manokinak River (4.9, 4.4-5.3) and Kokechik Bay (5.2, 4.7-5.6).

Apparent offtake and NAPP in grazing lawns.—Apparent offtake varied among locations and between years (Table 3). Apparent offtake was highest at Manokinak River and lower, but similar between Kokechik Bay and Old Chevak (Fig. 1). Between years, apparent offtake was greater in 2004 than 2003 (difference = 0.35g, SE = 0.08). At the end of the brood rearing period, above-ground biomass of vegetation that was not grazed (NAPP) was greater in 2004 than 2003 (difference = 0.41g, SE = 0.08), whereas the amount of biomass grazed was similar between years (difference = 0.05g, SE = 0.03). Furthermore, the biomass of grazed vegetation at the end of the brood rearing period in 2003 ($\overline{X} \pm SE$; 0.21 ± 0.02) and 2004 (0.28 ± 0.02) was similar to the initial amount in 2003 (0.20 ± 0.03) and 2004 (0.25 ± 0.03). Thus, despite annual variation in the amount of available biomass (NAPP), geese grazed vegetation to a common level. There was weak support for a model incorporating an interaction of location and year and for a

model with year only (Table 3). Summed Akaike weights were 1.0 and 0.88 for year and location, respectively.

Variation in body mass during 2003 – 2004.—Among goslings from Kokechik Bay, Manokinak River, and Old Chevak, body mass varied among locations, between years, and by sex (Table 4). A model that incorporated grazing lawn extent, interspecific densities of geese, and NAPP explained 89.4% of the deviance of the spatial (location) and temporal (year) variation but was not better supported by the data (Table 4). Estimates of body mass from the model that included an interaction of location and year were similar to those from the model incorporating interspecific densities, grazing lawn extent, and NAPP, indicating that these three variables accounted for most of the spatial and temporal variation in body mass (Fig. 2). Models incorporating interspecific densities received more support than those incorporating intraspecific densities (Table 4). Consistent with our predictions, body mass increased with grazing lawn extent, decreased with density, and increased slightly with NAPP, although we note that the slope coefficient for NAPP overlapped zero (Fig. 3).

Body mass was greatest at Old Chevak, intermediate at Kokechik Bay, and lowest at Manokinak River, but in 2003 goslings from Kokechik Bay were similar in body mass to those from Old Chevak (Fig. 2). Between years, body mass was greater in 2003, a year of low nest success, than 2004, but this difference was marginal at Old Chevak (Fig. 2). Body mass was greater for males than females (difference = 116.1g, SE = 18.5).

Relative hatch date effects.—The best approximating model indicated variation among locations, between years, by sex, and with relative hatch date (Table 5). This

model received almost twice as much support as the next best model (w = 0.27). We detected a decline in body mass with later hatch date ($\beta_{\text{relative hatch date}}$ = -16.1g, SE = 7.9). Body mass was greater for males than females (difference = 89.5g, SE = 22.9). Because patterns of variation in body mass were generally constant across the top models, we calculated estimates only from the best model. Estimates of body mass were greater in 2003 than 2004 and greater at Old Chevak than Manokinak River (Fig. 4). Thus, patterns of variation in body mass, after controlling for age and relative hatch date, were similar to the analysis of unmarked goslings. However, we note that the difference in body mass of known-age goslings between 2003 and 2004 was marginal (Fig. 4). Estimates of body mass from Manokinak River were highest in 1993 and 1994 and lowest in 2002.

Variation in body mass during 1990 – 2004.—The best approximating model indicated that body mass varied among locations, between years of low and high nest success, and by sex (Table 6). A trend in year was not supported by the data (Table 6). The model incorporating interspecific densities of geese performed better (ΔAICc = 77.9) than the model incorporating intraspecific densities (ΔAICc = 211.6), although both models received no support when contrasted with the location by years of low and high nest success model (Table 6). Estimated annual process variation ($\hat{\sigma}$) in body mass was 133.6g indicating large temporal variation.

Body mass was greatest at Old Chevak, intermediate at Kokechik Bay, and lowest at Manokinak River (Fig. 5). Estimates of body mass were higher in years when nest success was low; however, the magnitude of this difference varied among locations (Fig. 5). These estimates were consistent with the prediction that body mass was inversely

related to nest success. Body mass declined with increasing interspecific goose densities ($\beta_{density}$ = -33.5g, SE = 1.5). Males had greater body mass than females (difference = 105.6g, SE = 9.9).

DISCUSSION

Interspecific competition for forage.—Our findings indicate significant spatial and temporal variation in body mass. During 2003 – 2004, such variation was associated with the per capita availability of forage, which was a function of forage quantity and interspecific densities of geese. Although we were unable to incorporate densities of Black Brant, our documentation of the effects of interspecific densities (Cackling and Emperor Geese) is consistent with a previous study (Schmutz and Laing 2002) and further suggests that interspecific competition, and its effects on body mass, may be relevant across the principal breeding range of Emperor Geese. We do not believe this interspecific competition reflects differences in the competitive ability of these species, but rather that it is largely manifested through a type of exploitative competition (Gotelli 1998), whereby populations depress one another through use of a shared resource, in this case food. For instance, in 2003 and 2004, we detected similar amounts of initial and grazed above-ground biomass in grazing lawns, indicating that geese consumed ≥ 90% of the NAPP that occurred during brood rearing. Furthermore, NAPP was higher in 2004 and we correspondingly detected higher apparent offtake in that year, suggesting that even with increased NAPP food was still limiting.

Trends in densities of nesting geese.—Densities of Cackling Geese were variable among locations, but across locations increased from 1990 until about 1996 and then

remained relatively constant. In contrast, densities of Emperor Geese were relatively constant over time, except at Kokechik Bay. Thus, the interspecific competition we documented may be due to increased densities of Cackling Geese, which have led to a progressive shift and greater use of less-preferred habitats, such as those used by Emperor Geese (Schmutz 2001, Schmutz and Laing 2002).

Although our density estimates had large coefficients of variation and were not corrected for detection probability (Rosenstock et al. 2002), we believe the trends we observed reflect actual variation in density. Unless detection probability varied spatially or temporally, relative differences among locations or years should reflect true variation in density. We can think of no apparent reason why detection should vary spatially in this ecosystem. Habitats are similar across sampled locations, and little growth of any vegetation, which might contribute to variation in detection probability, has begun when surveys are conducted. We believe that the temporal trends were a consequence of changes in survival rates. In life-histories of geese, perturbations to adult survival are expected to have the largest proportional effect on population growth rate (Schmutz et al. 1997). Survival of adult Cackling Geese increased in the late 1980s and early 1990s, concurrent with perturbations of hunter harvest, (Raveling et al. 1992, U.S. Fish and Wildlife Service unpubl. data), whereas adult survival of Emperor Geese has not changed (Petersen 1992, Schmutz et al. 1994, Schmutz and Morse 2000, J. Schmutz unpubl. data). Evidence for increasing numbers in response to increased recruitment are less compelling, especially given density-dependent effects on growth of Emperor Geese (Schmutz and Laing 2002, this study) and Cackling Geese (C. Ely unpubl. data).

Dispersal or immigration also does not seem a tenable explanation for trends as the survey area encompasses ≥90% of the breeding area for both populations (King and Derksen 1986).

Patterns of variation in body mass.—We detected spatial variation in all analyses and during 2003 – 2004, body mass increased with grazing lawn extent, declined with interspecific goose densities, and increased slightly with NAPP. These patterns were consistent with past studies (Schmutz and Laing 2002, Person et al. 2003). The greatest body mass was observed at Old Chevak, which had the lowest density of geese coupled with a moderate amount of grazing lawn (3.3%). Body mass was lowest at Manokinak River, where grazing lawn extent was lowest (1.8%) and densities of geese were high and similar to Kokechik Bay, which had the greatest extent of grazing lawns (7.0%). Further, grazing intensity (apparent offtake) was highest at Manokinak River, and lower but similar between Old Chevak and Kokechik Bay, perhaps in response to densities of geese and grazing lawn extent at those locations.

Assessing the relative importance of forage and densities of geese to body mass of prefledging emperor geese is difficult, however, because of positive feedbacks between the two. For example, grazing by geese can improve quantity of vegetation through increases in NAPP (Cargill and Jefferies 1984, Hik and Jefferies 1990, Hik et al. 1991) and may exert strong influence on the dynamics of some grazing lawn communities (Ruess et al. 1997, Person et al. 2003). However, the density-dependent decline in body mass we documented further supports a direct association between food abundance and body mass. These results could also have been affected by variation in nitrogen content,

which we did not measure. We do not believe that observed variation in body mass reflects a significant genetic component of growth. Most evidence suggests that variation in growth of arctic and sub-arctic geese is largely environmentally influenced (Cooch et al. 1991a, Sedinger et al. 1997, Herzog 2002).

Similar to studies of geese in other populations (Cooch et al. 1991a, b, Larsson and Forslund 1991, Sedinger and Flint 1991), later hatched goslings had lower body mass. Such declines are largely mediated by seasonal reductions in per capita forage quality and quantity (Lindholm et al. 1994, Leafloor et al. 1998, Lepage et al. 1998). After controlling for relative hatch date and age, patterns of variation in body mass between marked and unmarked goslings were similar, suggesting that our estimate of age for unmarked goslings was not biased.

Temporal declines in prefledging body mass have previously been attributed to long-term increases in goose density (Cooch et al. 1991b, Sedinger et al. 1998). Overall, numbers of Cackling Geese increased 2.5 – 3x since 1985 (Eldridge 2003), and more than doubled since 1990 in locations we sampled, whereas numbers of Emperor Geese have remained relatively constant. We did not detect a negative linear trend in body mass when contrasted with a model that incorporated years when overall nest success was low or high. Body mass was inversely related to nest success, and was highest in 1990 and 2003. It is unlikely that this pattern was influenced by nest success itself, but rather the change in densities of broods and competition for food that resulted from variation in nest success. Furthermore, we suggest that this pattern was strongly driven by changes in interspecific densities of geese (not just Emperor Geese). Arctic foxes (*Alopex lagopus*)

are the primary, terrestrial predator of nests, and in some years the proximate cause of large-scale nest failure on the Yukon-Kuskokwim Delta. Cackling Geese experienced higher rates of nest failure (Fischer et al. 2004), resulting in disproportionate reductions relative to Emperor Geese.

During 1990 – 2004, evidence was stronger for the effects of interspecific densities of geese on body mass than intraspecific densities. However, models incorporating both these effects performed poorly when contrasted with more general spatial (location) and temporal (years of low and high nest success) variation. This poor performance may have been related to variation in NAPP and grazing lawn extent, which we could not account for in all years, but were important in describing variation in body mass during 2003 – 2004. Geese consumed virtually all the NAPP in grazing lawns that occurred during brood rearing; despite this, the amount of NAPP varied spatially and temporally. Grazing lawn extent had a larger influence on body mass than NAPP and we suspect that grazing lawn extent may have declined from earlier levels. The extent of grazing lawns is dynamic and has been related to a positive feedback with densities of the herbivore population (Person et al. 2003). Densities of Cackling Geese increased from 1985 until about 1996 and then reached relative stability, whereas densities of Emperor Geese have remained relatively constant (Eldridge 2003). Recent stability in population size coupled with annual variation in densities of broods from low nest success (Fischer et al. 2004), could have led to a reduction in the grazing pressure needed to create and maintain grazing lawns (Ruess et al. 1997, Person et al. 2003). In fact, a related study documented a slight decline in the extent of grazing lawns during 1999 – 2004 (Chapter

1). Such a decline could partially explain the strong influence of annual variation in nest success on body mass because in recent years of high nest success, it is probable that the per capita limitation of forage is exacerbated, resulting in stronger competition for forage.

Changes in the fall age ratio and future considerations for management.—The decline in the fall age ratio of Emperor Geese (Anderson et al. 2003) is suggestive of reduced survival of juveniles. For the range of annual variation in body mass observed, survival models for juvenile female Emperor Geese (Schmutz 1993, J. Schmutz unpubl. data) predicted a difference in apparent survival to fall staging areas of 0.45. We suggest that the fall age ratio has declined, in part, because of reduced body mass from interspecific competition during brood rearing. We further suggest that interspecific effects on body mass occur broadly, across the Yukon-Kuskokwim Delta as the three locations we sampled are representative of a range of variation in goose densities (U.S. Fish and Wildlife Service unpubl. data) and grazing lawn extent (Chapter 1). The fall age ratio may also be affected by other parameters, such as annual variation in gosling survival (Schmutz et al. 2001) or nest success (Fischer et al. 2004). However, high rates of gosling survival or nest success may be offset by reductions in juvenile survival from density-dependent declines in prefledging body mass.

Spatial and temporal variation in body mass was most strongly affected by grazing lawn extent and interspecific densities of geese. The broad scale at which we measured these variables makes dispersal to higher-quality locations unlikely as philopatric behavior in geese is relatively strong (Lindberg and Sedinger 1998, but see Cooch et al. 1993). Management to increase the population size of Emperor Geese needs

to consider interspecific densities and interactions between densities and forage. The potential for positive feedbacks between goose densities and grazing lawn extent (Person et al. 2003) increases the complexity of such interactions. To elucidate these complex interactions, landscape-level monitoring of the food resources and goose densities is needed.

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TABLE 1. Numbers of prefledging Emperor Geese captured by year, location, and sex. Numbers in parentheses indicate the number of known-age goslings recaptured.

Year	Kokechik Bay		Manokinak River		Old Chevak	
	Female	Male	Female	Male	Female	Male
1990	140	165	53	57	14	12
1993	0	0	78 (21)	76 (19)	0	0
1994	0	0	32 (5)	28 (6)	0	0
1995	0	0	60	56	0	0
1996	0	0	26	36	37	35
2002	0	0	11(8)	11 (8)	19	22
2003	14	9	34 (7)	32 (2)	41 (4)	29 (5)
2004	25	21	35 (13)	17 (8)	76 (6)	86 (12)
Total	179	195	329 (54)	313 (43)	187 (10)	184 (17)

TABLE 2. Nesting densities (indicated pairs/km^2) of Cackling Geese and Emperor Geese from 1990 – 2004 at Kokechik Bay, Manokinak River, and Old Chevak. Estimates are means with 95% confidence intervals in parentheses.

Year	Kokechik Bay		Manokinak River		Old Chevak	
	Cackling Geese	Emperor Geese	Cackling Geese	Emperor Geese	Cackling Geese	Emperor Geese
1990	10.6 (-1.2 – 22.3)	2.7 (1.2 – 4.3)	8.8 (3.2 – 14.4)	3.5 (1.3 – 5.8)	7.0 (1.0 – 13.1)	1.3 (-0.1 – 2.8)
1991	8.5 (1.9 – 15.2)	2.2 (0.9 – 3.5)	10.4 (5.7 – 15.2)	3.9 (3.0 – 4.8)	7.5 (3.4 – 11.6)	2.0 (0.9 – 3.0)
1992	13.9 (1.1 – 26.7)	3.5 (1.8 – 5.1)	12.5 (6.7 – 18.3)	4.2 (2.2 – 6.2)	11.7 (5.4 – 18.1)	1.5 (0.4 – 2.7)
1993	13.0 (5.0 – 21.1)	3.6 (3.1 – 4.2)	12.3 (7.7 – 16.9)	3.6 (1.9 – 5.3)	14.7 (7.5 – 21.9)	2.6 (1.6 – 3.6)
1994	17.7 (10.4 – 25.1)	4.6 (3.2 – 6.0)	19.5 (10.9 – 28.2)	6.5 (5.2 – 7.8)	13.0 (6.3 – 19.7)	3.0 (1.6 – 4.4)
1995	21.1 (11.8 – 30.4)	4.9 (3.1 – 6.7)	25.4 (16.5 – 34.2)	6.1 (3.7 – 8.4)	16.9 (9.4 – 24.4)	2.6 (0.9 – 4.3)
1996	21.4 (5.9 – 37.0)	5.5 (4.0 – 7.1)	22.5 (11.8 – 33.3)	5.9 (3.3 – 8.5)	14.7 (5.4 – 24.0)	2.5 (1.7 – 3.2)
1997	19.8 (10.7 – 29.0)	7.4 (6.0 – 8.7)	25.7 (18.4 – 33.0)	5.0 (3.9 – 6.1)	14.2 (6.4 – 22.0)	2.9 (1.6 – 4.2)
1998	14.4 (7.4 – 21.4)	4.9 (3.7 – 6.1)	20.2 (14.1 – 26.4)	5.1 (3.9 – 6.3)	11.8 (8.5 – 15.2)	2.5 (1.7 – 3.3)
1999	24.4 (13.5 – 35.4)	6.4 (4.2 – 8.7)	25.9 (13.2 – 38.5)	5.2 (3.2 – 7.3)	10.2 (6.2 – 14.1)	2.7 (0.7 – 4.7)
2000	21.5 (12.5 – 30.5)	6.0 (3.7 – 8.4)	22.8 (17.7 – 27.9)	4.1 (2.1 – 6.1)	17.6 (10.8 – 24.4)	3.5 (2.6 – 4.5)
2001	20.6 (9.4 – 31.7)	6.0 (4.1 – 7.9)	28.4 (14.8 – 41.9)	6.2 (4.0 – 8.4)	13.1 (8.8 – 17.5)	3.2 (1.9 – 4.5)
2002	17.9 (14.3 – 21.7)	5.8 (4.0 – 7.6)	19.2 (12.2 – 26.2)	4.4 (2.0 – 6.7)	11.6 (6.0 – 17.1)	2.7 (1.9 – 3.5)
2003	19.4 (8.1 – 30.6)	5.1 (4.3 – 5.9)	21.2 (14.8 – 27.6)	5.0 (3.1 – 7.0)	12.2 (3.3 – 21.2)	2.1 (0.9 – 3.3)
2004	20.8 (12.9 – 28.7)	7.8 (5.1 – 10.5)	19.3 (11.1 – 27.4)	4.3 (2.8 – 5.8)	11.7 (6.1 – 17.3)	3.4 (1.4 – 5.5)

TABLE 3. Model selection results for analysis of variation in apparent offtake. Models are ranked by relative differences in $\Delta AICc$ values and we present all models with $\Delta AICc \leq 4$. Data were collected at Kokechik Bay, Manokinak River, and Old Chevak during 2003 – 2004.

Fixed effects[a]	K[b]	-2log(L)	$\Delta AICc$	w[c]
Location + Year	6	48.2	0.0	0.64
Location * Year	8	45.1	2.0	0.24
Year	4	56.1	3.3	0.12

[a]The "+" between variables indicates an additive effect; the "*" denotes an interaction

[b]Number of fixed-effect and covariance parameters

[c]Weight of evidence for being the best approximating model

TABLE 4. Model selection results for analysis of body mass during 2003 – 2004. Locations included Kokechik Bay, Manokinak River, and Old Chevak. Models are ranked by relative differences in $\Delta AICc$ values. We present all models with $\Delta AICc \leq 4$, the best model incorporating interspecific goose densities (combined density of Emperor and Cackling Geese), grazing lawn extent, and NAPP, and the best model incorporating intraspecific goose densities (density of Emperor Geese only), grazing lawn extent, and NAPP.

Fixed effects[a]	K[b]	-2log(L)	$\Delta AICc$	w[c]
Location * Year + Sex	8	-360.8	0.0	1.00
Interspecific densities + grazing lawn extent + NAPP + Sex	6	-340.4	16.2	0.00
Intraspecific densities + grazing lawn extent + NAPP + Sex	6	-310.7	45.9	0.00

[a]The "+" between variables indicates an additive effect; the "*" denotes an interaction

[b]Number of fixed-effect and covariance parameters

[c]Weight of evidence for being the best approximating model

TABLE 5. Model selection results for analysis of relative hatch date effects on body mass. Data were collected at Manokinak River during 1993 – 1994, 2002 – 2004, and Old Chevak during 2003 – 2004. Models are ranked by relative differences in $\Delta AICc$ values and we present all models with $\Delta AICc \leq 4$.

Fixed effects[a]	K[b]	-2log(L)	$\Delta AICc$	w[c]
Location + Year + Sex + Relative hatch date	10	1565.9	0.0	0.27
Location * Year + Sex + Relative hatch date	11	1564.6	1.1	0.16
Location + Year + Sex + Relative hatch date * Year	14	1557.2	1.1	0.16
Location + Year + Sex	9	1570.0	1.7	0.12
Location * Year + Sex + Relative hatch date * Year	15	1555.7	2.2	0.09
Location * Year + Sex	10	1568.3	2.3	0.09
Location + Year + Sex + Relative hatch date + Relative hatch date^2	11	1565.9	2.4	0.08
Location * Year + Sex + Relative hatch date + Relative hatch date^2	12	1564.6	3.5	0.05

[a]The "+" between variables indicates an additive effect; the "*" denotes an interaction

[b]Number of fixed-effect and covariance parameters

[c]Weight of evidence for being the best approximating model

TABLE 6. Model selection results for analysis of body mass during 1990 – 2004. Locations included Kokechik Bay, Manokinak River, and Old Chevak. Models are ranked by relative differences in ΔAICc values. We present all models with ΔAIC$c \leq 4$, the best linear time trend model, the model incorporating interspecific goose densities (combined density of Emperor and Cackling Geese), and the model incorporating intraspecific goose densities (density of Emperor Geese only). Year was included as a random effect in all models.

Fixed effects[a]	K[b]	-2log(L)	ΔAICc	w[c]
Location * Low nest success years[d], high nest success years[e] + Sex	9	18352.9	0.0	1.00
Location * YEAR[f] + Sex	7	18386.0	29.1	0.00
Interspecific densities + Sex	5	18438.8	77.9	0.00
Intraspecific densities + Sex	5	18572.6	211.6	0.00

[a]The "+" between variables indicates an additive effect; the "*" denotes an interaction

[b]Number of fixed-effect and covariance parameters

[c]Weight of evidence for being the best approximating model

[d]Years when nest success was low or below average (1990, 2003)

[e]Years when nest success was high or above average (1993, 1994, 1995, 1996, 2002, 2004)

[f]Linear time trend

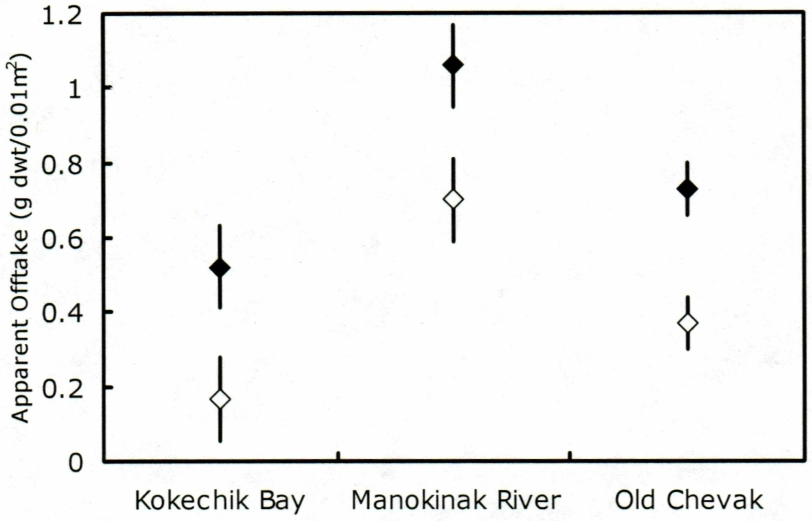

FIG. 1. Estimates of apparent offtake ($\overline{X} \pm SE$) in grazing lawns at Kokechik Bay, Manokinak River, and Old Chevak in 2003 (open diamonds) and 2004 (closed diamonds).

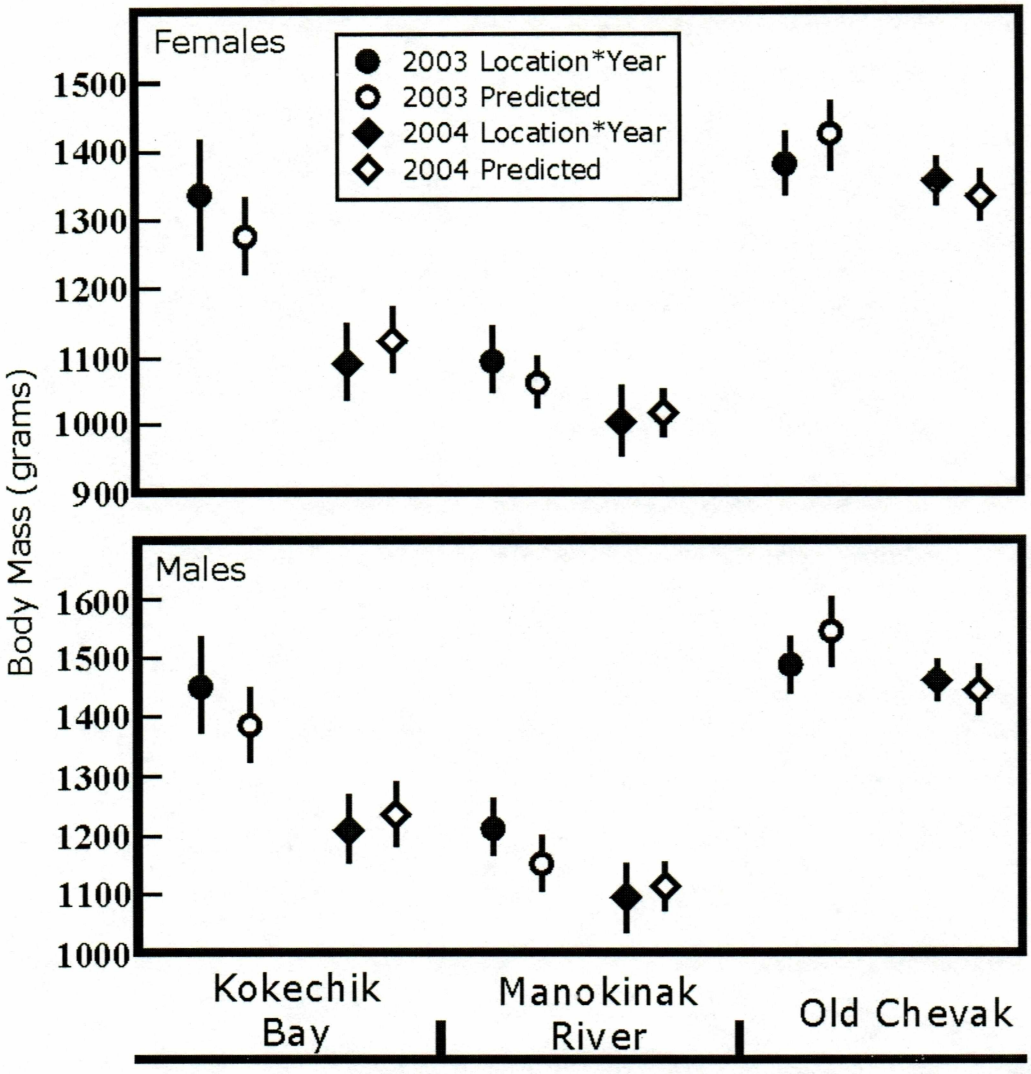

FIG. 2. Body mass (means and 95% confidence intervals) of prefledging Emperor Geese in 2003 and 2004 at Kokechik Bay, Manokinak River, and Old Chevak. Depicted are estimates from the general location*year model and the predicted values from the model where body mass was a function of interspecific goose densities, grazing lawn extent, and NAPP. The similarity in mass values from these two models demonstrates that interspecific goose densities, grazing lawn extent, and NAPP accounted for most of the spatial and temporal variation in body mass.

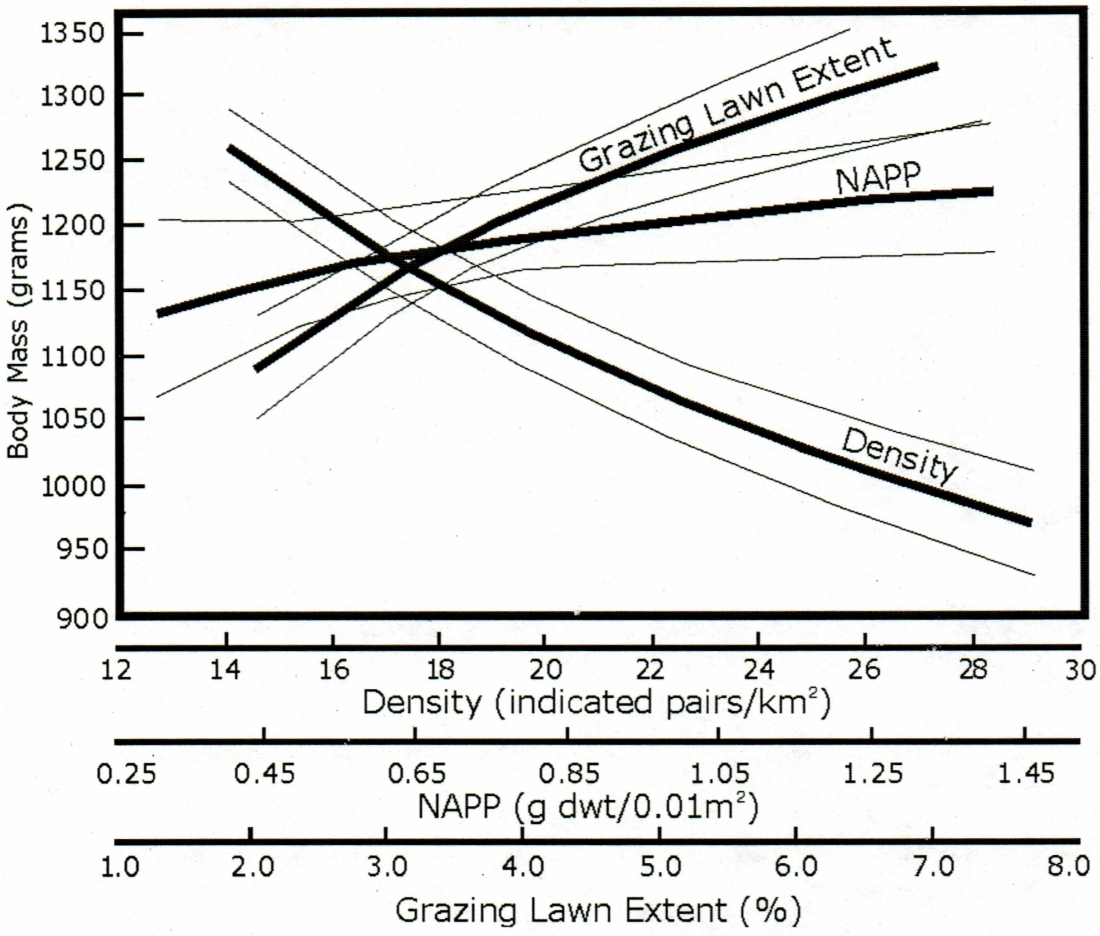

FIG. 3. The relationship between body mass and mean estimates of density of Cackling and Emperor Geese, grazing lawn extent, and NAPP. The trends are predicted by the parsimonious model: Body Mass = Density/Grazing Lawn Extent*NAPP + Sex, which was log-transformed prior to analysis. There was a constant difference between males and females, and trends are shown for females only. Lighter lines indicate 95% confidence intervals.

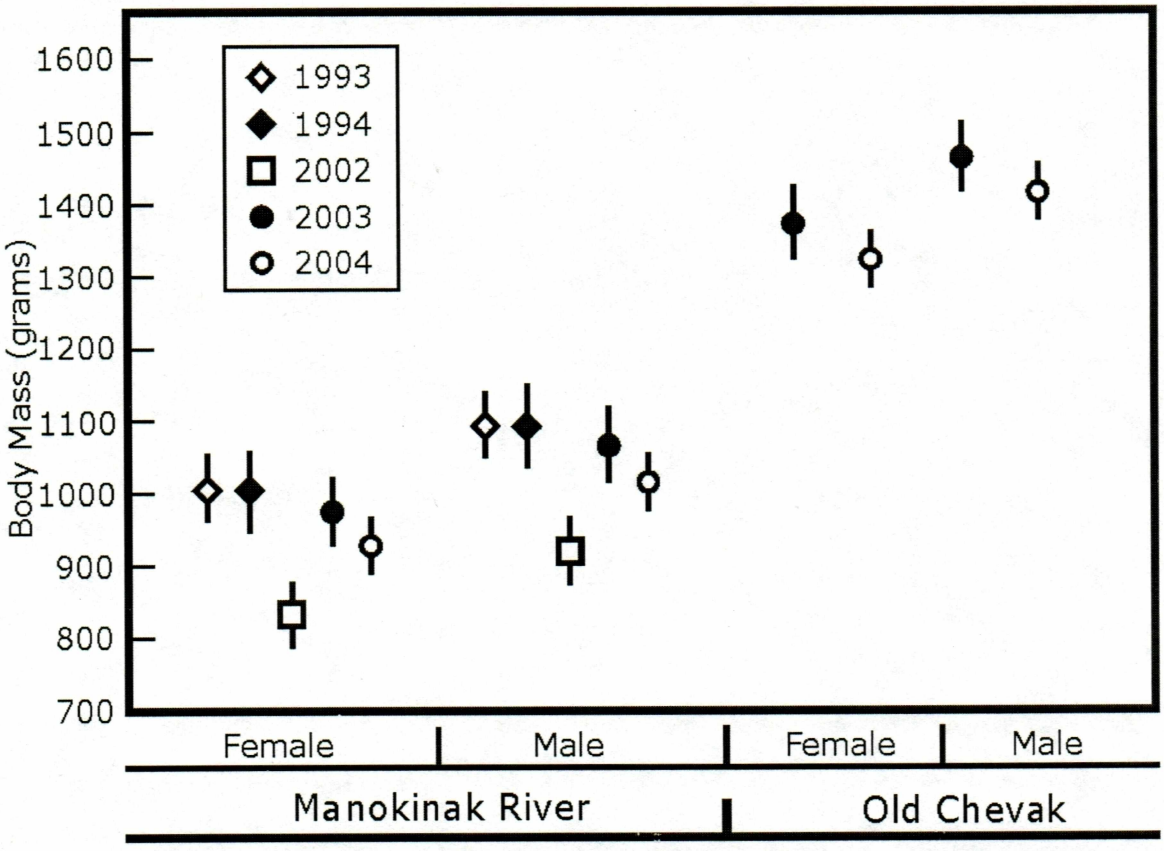

FIG. 4. Body mass ($\overline{X} \pm SE$) of known-age prefledging Emperor Geese at Manokinak River and Old Chevak, corrected for age and relative hatch date.

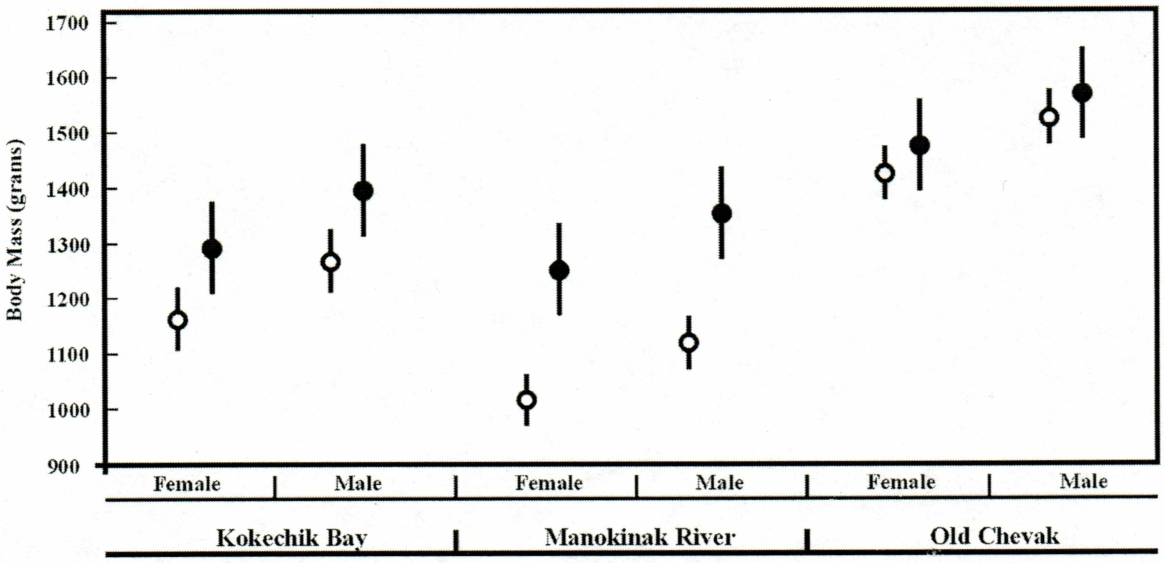

FIG. 5. Body mass ($\overline{X} \pm SE$) of prefledging Emperor Geese at Kokechik Bay, Manokinak River, and Old Chevak. Open circles represent years when nest success was high or above average (1993, 1994, 1995, 1996, 2002, 2004) and closed circles represent years when nest success was low or below average (1990 and 2003).

CONCLUSIONS

Body mass of prefledging emperor geese was affected by interspecific densities of geese (combined density of emperor and cackling geese), grazing lawn extent, and NAPP. This result supports that of Schmutz and Laing (2002) and further suggests that interspecific competition for forage is relevant at large spatial and temporal scales. Such competition should not be interpreted as reflecting differential competitive abilities of these species, but rather is likely a type of exploitative competition (Gotelli 1998), whereby populations depress one another through shared use of a resource, in this case food. For instance, grazing by geese during the brood rearing period resulted in consumption of $\geq$ 90% of the NAPP that occurred in grazing lawns. Further, I suspect that interspecific effects on body mass occur broadly, across the Yukon-Kuskokwim Delta, as the three locations I sampled are representative of a range of variation in goose densities (U.S. Fish and Wildlife Service unpubl. data) and grazing lawn extent (Chapter 1). Because of the positive relationship between prefledging body mass and survival to fall staging areas (Schmutz 1993), I suggest that declines during 1996 – 2003 in the fall age ratio may be partially from negative effects of interspecific goose densities on body mass. Management to increase the population size of emperor geese needs to consider interspecific densities of geese and interactions between interspecific densities and forage.

Across the three locations sampled (Kokechik Bay, Manokinak River and Old Chevak), estimates of density (mean/km^2, 95% confidence interval) for Cackling Geese more than doubled from 1990 (9.0, 4.8-13.2) to 1996 (19.9, 13.3-26.6) and appeared to be

relatively stable from 1996 to 2004 (17.9, 13.7-22.0). In contrast, densities of Emperor Geese were ~2 – 5x lower and were generally similar among years, except at Kokechik Bay, where densities were 2.7 (1.2-4.3) in 1990, 5.5 (4.0-7.1) in 1996, and 7.8 (5.1-10.5) in 2004. Thus, the interspecific competition I documented may be due to increased densities of Cackling Geese, which have led to a progressive shift into less-preferred habitats, such as those used by Emperor Geese (Schmutz 2001, Schmutz and Laing 2002). Among locations, densities of Cackling and Emperor Geese were lowest at Old Chevak and higher but similar between Kokechik Bay and Manokinak River.

Using aerial videography, I classified grazing lawns with an accuracy >91%. The ability to accurately identify fine-scale, patchily distributed habitats across a large geographic region increases the applicability of this method to other ecosystems.

During 1999 – 2004 the extent of grazing lawns was stable or slightly decreased, among- and within-locations. Grazing lawn extent is dynamic and related to both past and present densities of the herbivore population (Person et al. 2003), and during the years of my study, the population size of herbivores in the composite goose community was relatively stable. This stability coupled with recent annual variation in the numbers of goose broods from low nest success (Fischer et al. 2004) may explain the slight decline in grazing lawn extent. It is probable that grazing pressures in years of low nest success were insufficient for maintenance of grazing lawns (Ruess et al. 1997, Person et al. 2003). A decline in grazing lawn extent may reduce the per capita availability of this resource to prefledging emperor geese.

Grazing lawn extent varied substantially among locations; mean estimates (± SE) ranged from 1.8% (0.66) to 7% (0.67). Such large variation likely contributes to variation in the body mass emperor geese achieve prior to fledging. Within locations, grazing lawn extent was 4% (SE = 0.80) higher adjacent to ponds than rivers. This result has implications for land-cover change because in Arctic ecosystems change in the amount of ponds and lakes has been most pronounced (Stow et al., 2004). Pond recession, like that observed in 2003 and 2004 (B. Lake pers. observation), may have large influence on this resource in the future.

During 2003 – 2004, body mass of prefledging emperor geese increased with grazing lawn extent (Person et al. 2003) and NAPP and declined with interspecific densities of geese (Schmutz and Laing 2002). These three variables explained a substantial amount (89.4%) of the deviance from a model that incorporated more general spatial (location) and temporal (year) variation. Although assessing the relative importance of forage and densities of geese is difficult because of positive, lagged, feedbacks between the two (Hik and Jefferies 1990, Person et al. 2003), the density-dependent decline in body mass we documented further supports a direct association between food abundance and body mass. During 1990 – 2004, body mass was inversely related to nest success and declined with interspecific goose densities, indicating the importance of goose densities to long-term variation in body mass.

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